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Silvical Characteristics of Engelmann Spruce

Robert R. Alexander and Wayne D. Shepperd

Abstract

This report summarizes information on distribution, botanical description, habitat conditions, life history, special uses, and genetics of Engelmann spruce.

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Silvical Characteristics of Engelmann Spruce

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Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) is one of seven species of spruce indigenous to the United States (Little 1979). Other common names are Columbian spruce, mountain spruce, white spruce, silver spruce, and pino real (fig. 1).

Engelmann spruce—subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests occupy the highest water yielding areas in the Rocky Mountains. They also provide timber, habitats for a wide variety of game and nongame wildlife, forage for livestock, and recreational opportunities and scenic beauty (Alexander 1977). However, these values are indigenous to where spruce grows rather than to any special properties associated with Engelmann spruce.

DISTRIBUTION

Engelmann spruce is widely distributed in the western United States and two provinces in Canada (Little 1971). Its range extends from British Columbia and Alberta, Canada, south through all western states to New Mexico and Arizona (fig. 2).

Figure 1.—Mature Engelmann spruce on the Fraser Experimental Forest, Colorado.

In the Pacific Northwest, Engelmann spruce grows along the east slope of the Coast Range from west-central British Columbia, south along the crest and east slope of the Cascades through Washington and Oregon to northern California (Alexander 1958, 1965, 1980). It is a minor component of these high elevation forests.

Engelmann spruce grows in the Rocky Mountains of southwestern Alberta, south through the high mountains of eastern Washington and Oregon, Idaho, western Montana, to western and central Wyoming, and in the high mountains of southern Wyoming, Colorado, Utah, eastern Nevada, New Mexico, and northern Arizona (Alexander 1958, 1965, 1980). It is a major component of the high elevation Rocky Mountain forests.

BOTANICAL DESCRIPTION

The botanical features of Engelmann spruce, as described by McSwain et al. (1970) and Preston (1948), are as follows:

Needles.—Needles are 1 to 1–1/4 inches long, petioled, flexible, four-sided, usually blue green with an occasional whitish glaucous bloom. Tips are blunt or acute. Needles tend to be crowded on the upper side of the branch because those on the lower side are curved upwards (fig. 3A).

Flowers.—Male flowers are dark purple; female, bright scarlet. Each is borne separately in the crown (fig. 3A).

Cones.—The cones are usually 1 to 2–1/2 inches long, light chestnut brown when ripe, and ovate to cylindrical in shape. Cones are sessile or short-stalked with thin, somewhat papery, wedge-shaped scales, commonly notched at the apex (fig. 3B).

Seeds.—The dark brown to nearly black seeds average 1/8 inch long, with a broad oblique wing about 1/2 inch long (fig. 3B).

Twigs.—The minutely pubescent, rather stout twigs are orange brown to gray brown.

Winter buds.—The pale chestnut brown winter buds are broadly ovoid to conic, and average 1/8 to 1/4 inch long.

Bark.—The bark is very thin and broken into large, purplish-brown to russet-red, loosely attached scales (fig. 3C).

Wood.—Heartwood is nearly white with an occasional tinge of red. Sapwood is narrow—3/4 to 2 inches wide in sawtimber—and difficult to distinguish from heartwood, but it is commonly lighter in color. The wood is generally straight-grained, lightweight, medium stiff, soft, fine-textured, and without odor or taste. It has

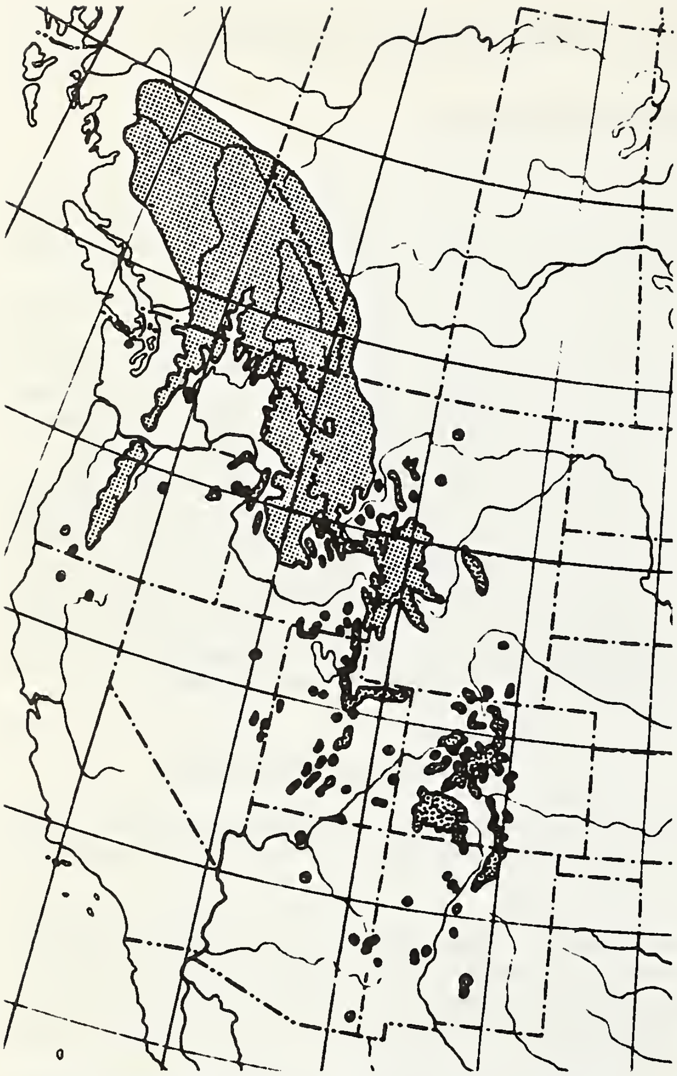

Figure 2.—Natural range of Engelmann spruce. (Little 1971)

moderately low shrinkage, can be readily air-dried, and is easy to work. Resin ducts are few, but distinguish the wood from true firs.

HABITAT CONDITIONS

Climate

Engelmann spruce grows in a cool and humid climate, with long, cold winters and short, cool summers (Thornthwaite 1948). It occupies one of the highest and coldest forest environments in the western United States, characterized by heavy snowfall and temperature extremes of more than −50° F to above 90° F. Climatic data for four subregions of the United States within the species range are given in table 1 (Baker 1944, Haeffner 1971, Marr et al. 1968).

The range of mean annual temperatures is narrow considering the wide distribution of the species. Average annual temperatures are near freezing and frost may occur any month of the year. Average precipitation exceeds 24 inches annually, with only

Figure 3.—Botanical features of Engelmann spruce: A, needles and male flowers; B, mature and immature cones and seeds; C, bark.

Table 1.—Climatological data for four regional subdivisions within the range of Engelmann spruce

Location	Average temperature			Annual precipitation	Annual snowfall	Frostfree period
	Annual	July	January			
	°F	°F	°F	*inches*	*inches*	*days*
Pacific Northwest	35	50-55	15-20	60-160	400 +	45-90
U.S. Rocky Mountains						
Northern[1]	30-35	45-55	10-20	24-45 +	250 +	[4]30-60
Central[2]	30-35	50-55	10-15	24-55	150-350 +	[4]30-60
Southern[3]	35	50-60	15-20	24-35 +	200 +	[4]30-60

[1] *Includes the Rocky Mountains of Montana and Idaho and associated mountains of eastern Washington and Oregon.*
[2] *Includes the Rocky Mountains of Wyoming and Colorado and associated mountains of Utah.*
[3] *Includes the Rocky Mountains and associated ranges of New Mexico and Arizona and the plateaus of southern Utah.*
[4] *Frost may occur any month of the year.*

moderate or no seasonal deficiency. Summer is the driest season in the Cascades and Rocky Mountains west of the Continental Divide south to southwestern Colorado. The mountains east of the divide, in southwestern Colorado, southern Utah, and in New Mexico and Arizona, receive considerable summer rainfall, while winter snowfall can be relatively light (Baker 1944, Johnson and Cline 1965, Marr 1961, Thornthwaite 1948). Winds are predominately from the west and southwest and can be highly destructive to Engelmann spruce (Alexander 1964, Alexander and Buell 1955, Daubenmire 1943).

Soils

Information on soils where Engelmann spruce grows is limited. In the Pacific Coast region, soil parent materials are mixed and varied. Country bedrock is composed of a variety of sedimentary, igneous, and metamorphic rock. The most common of the great soil groups are Cryorthods (Podzolic soils), Haplumbrepts (western Brown forest soils), Haplorthods (Brown Podzolic soils), Hapludalfs (Gray-Brown Podzolic soils), and Haploxerults and Haplohumults (Reddish-Brown Lateritic soils); these great soil groups developed from deep glacial and lacustrine deposits, deep residual material weathered in place from country rock, and volcanic lava and ash. Xerochrepts (Regosolic soils) developed from shallow residual material are also widespread. Xeropsamments (Regosolic soils) and Haplaquolls (Humic Gley soils) are the principal soils derived from alluvium. On the east side of the Cascade crest, soils are largely Haploxeralfs (Non-Calcic Brown soils) and Haploxerolls (Chestnut soils) (Franklin and Dyrness 1973, USDA SCS 1975).

In the Rocky Mountain subalpine zone, soil materials vary according to the character of the bedrock from which they originated. Crystalline granite rock predominates, but conglomerates, shales, sandstones, basalts, and andesites commonly occur. Glacial deposits and stream alluvial fans are also common along valley bottoms. Of the great soils group, Cryorthods (Podzolic soils) and Haplorthods (Brown Podzolic soils) occur extensively on all aspects. Dystrochrepts (Sols Brun Acides) occur extensively on the drier aspects. Aquods (Ground-Water Podzolic soils) are found in the more poorly drained areas, Eutroboralfs (Gray-Wooded soils) are found where timber stands are less dense and parent material finer textured. Eutrochrepts (Brown Forest soils) occur mostly in the lower subalpine along stream terraces and side slopes. Lithics (Lithosolic soils) occur whenever bedrock is near the surface. Dystrandepts (Bog soils), and Haplaquepts (Humic Gley soils) occur extensively in poorly drained upper stream valleys (Johnson and Cline 1965, USDA SCS 1975).

Regardless of the great soil groups associated with spruce stands, it grows best on moderately deep, well-drained, loamy sands and silts, and silt and clay loam soils developed from volcanic lava flows and sedimentary rock. Good growth is also made on alluvial soils developed from a wide range of parent materials, where an accessible water table is more important than physical properties of the soil. It does not grow well on shallow, dry, coarse-textured sands; gravels developed primarily from granitic and schistic rock; coarse sandstones and conglomerates; rocky glacial till; heavy clay surface soils; or saturated soils (Alexander 1958, 1965).

Topography

Along the east slope of the Coast Range and interior valleys of southwestern British Columbia, Engelmann spruce grows at 2,500 to 3,500 feet. Farther south in the Cascade Mountains of Washington and Oregon, it generally grows at 4,000 to 6,000 feet, but may be found at 8,000 feet on sheltered slopes, and at 2,000 feet in cold pockets along streams and valley bottoms. In northern California, it is found at 4,000 to 5,000 feet (Alexander 1980, Sudworth 1916).

South of the Peace River Plateau in the Canadian Rocky Mountains of western British Columbia and Alberta, Engelmann spruce grows at 2,500 to 6,000 feet;

in the Rocky Mountains of Idaho and Montana, and in the adjacent mountains of eastern Washington and Oregon, at 2,000 to 9,000 feet. But above 6,000 to 7,500 feet, it is a minor component of the stand, and below 5,000 feet it is confined to moist, lower slopes and cold, valley bottoms (Alexander 1958, 1965).

Engelmann spruce is found at 9,000 to 11,000 feet in the Rocky Mountains of Utah, Wyoming, and Colorado, but may extend as low as 8,000 feet along cold stream bottoms and to timberline at 11,500 feet. In the Rocky Mountains of New Mexico and Arizona and on the plateaus of southern Utah, it grows at 9,500 to 11,000 feet but may grow as low as 8,000 feet and as high as 12,000 feet (Bates 1924, Marr 1961, Pearson 1931).

Associated Vegetation

Trees

Engelmann spruce most typically grows together with subalpine fir to form the Engelmann spruce—subalpine fir type (SAF Type 206) (Society of American Foresters 1980). It may also occur in pure or nearly pure stands. Spruce grows in 15 other forest cover types recognized by the Society of American Foresters, usually as a minor component or in frost pockets:

SAF Type Number	Type
201	White Spruce
205	Mountain Hemlock
208	Whitebark Pine
209	Bristlecone Pine
210	Interior Douglas-fir
212	Western Larch
213	Grand Fir
215	Western White Pine
216	Blue Spruce
217	Aspen
218	Lodgepole Pine
219	Limber Pine
224	Western Hemlock
226	Coastal True Fir—Hemlock
227	Western Redcedar—Western Hemlock

Composition of forests in which Engelmann spruce grows is influenced by elevation, aspect, and latitude (Daubenmire 1943).[2] In the Rocky Mountains and Cascades, subalpine fir is its common associate at all elevations. In the northernmost part of its range along the Coast Range and in the Rocky Mountains of Canada, it mixes with white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill. B.S.P.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.). In the Rocky Mountains of Montana and Idaho, in the Cascades, and in the mountains of eastern Washington and Oregon, associates at lower and middle elevations are western white pine (*Pinus monticola* Dougl. ex D. Don), western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Biessn.) Franco), western larch (*Larix occidentalis* Nutt.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud). Associates at higher elevations are Pacific silver fir (*Abies amabilis* Dougl. ex Forbes), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr), subalpine larch (*Larix lyallii* Parl.), and whitebark pine (*Pinus albicaulis* Engelm.).

²Classification of forest vegetation into "habitat types" based on methodology developed by Daubenmire (1952) and modified by others is available for much of the western forested lands. The known habitat types for all lands where Engelmann spruce grows are listed in the appendix, with other descriptive material.

In the Rocky Mountains south of Montana and Idaho and in the mountains of Utah, lodgepole pine, Rocky Mountain Douglas-fir, blue spruce (*Picea pungens* Engelm.), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), quaking aspen (*Populus tremuloides* Michx.), and occasionally ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and southwestern white pine (*Pinus strobiformis* Engelm.) are common associates at lower and middle elevations, and corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.), limber pine (*Pinus flexilis* James), and bristlecone pine (*Pinus aristata* Engelm.) at higher elevations. Engelmann spruce extends to timberline in the Rocky Mountains south of Idaho and Montana and may form pure stands at timberline in the southernmost part of its range. In the Canadian Rockies of southwestern Alberta and adjacent British Columbia and into the Rocky Mountains north of Wyoming and Utah, and the Cascades, spruce usually occupies moist sites below timberline; its high-elevation associates form timberline forests (Alexander 1958, 1965, 1980).

Understory Vegetation

In the understory throughout much of the range of Engelmann spruce, Rocky Mountain maple (*Acer glabrum* Torr.), twinflower (*Linnaea borealis* L.), and heartleaf arnica (*Arnica cordifolia* Hook.) occur on cool, moist sites; myrtle boxleaf (*Pachistima myrsinites* (Pursh.) Raf.), elksedge (*Carex geyeri* Boott), and creeping juniper (*Juniperus communis* L.) occur on warm, dry sites; and grouse whortleberry (*Vaccinium scoparium* Michx.), mountain gooseberry (*Ribes montigenum* McClat.), and fireweed (*Epilobium angustifolium* L.) occur on cool, dry sites.

Species characteristically found in the Pacific Northwest Region, and the Rocky Mountains and associated ranges north of Utah and Wyoming include: Labrador tea (*Ledum glandulosum* Nutt.), Cascades azalea (*Rhododendron albiflorum* Hook.), rusty skunkbush (*Menziesia ferruginea* Smith), and woodrush (*Luzula hitchcockii* Hamet-Ahti) on cool, moist sites; starry solomon plume (*Smilacina stellata* (L.) Desf.), queenscup beadlily (*Clintonia uniflora* (Schult.) Runth), twistedstalk (*Streptopus amplexifolius* (L.) D.C.), and sweetscented bedstraw (*Galium triflorum* Michx.) on warm, moist sites; dwarf huckleberry (*Vaccinium caespitosum* Michx.), and blue huckleberry (*Vaccinium globulare*

Rydb.) on cool, dry sites; beargrass (*Xerophyllum tenax* (Pursh.) Nutt.), white spirea (*Spiraea betulifolia* Hook.), pinegrass (*Calamagrostis rubescens* Buckl.), and big whortleberry (*Vaccinium membranaceum* Dougl.) on warm, dry sites; and marshmarigold (*Caltha leptosepala* D.C.), devilsclub (*Oplopanax horridum* (J.E. Smith) Miq.), and bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on wet sites (Daubenmire and Daubenmire 1968, Franklin and Dyrness 1973, Pfister 1972, Pfister et al. 1977, Steele et al. 1981, 1983).

Understory vegetation characteristically found in the Rocky Mountains and associated ranges south of Idaho and Montana include: mountain bluebells (*Mertensia ciliata* (James) G. Don) and heartleaf bittercress (*Cardamine cordifolia* Gray) on cool, moist sites; red buffaloberry (*Shepherdia canadensis* (L.) Nutt.), Oregon grape (*Berberis repens* Lindl.), daisy fleabane (*Erigeron superbus* Rydb.), and Arizona peavine (*Lathyrus arizonicus* Britt.) on warm, dry sites; and Rocky Mountain whortleberry (*Vaccinium myrtillus* L.), groundsel (*Senecio sanguisorboides* Rydb.), polemonium (*Polemonium pulcherrimum* Hook.), prickly currant (*Ribes lacustre* (Pers.) Poir), sidebells pyrola (*Pyrola secunda*), and mosses on cool, dry sites (Alexander et al. 1984a, Hess 1981, Hoffman and Alexander 1976, 1980, 1983, Moir and Ludwig 1979, Wirsing and Alexander 1975).

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting

Engelmann spruce is monoecious, with ovulate strobili usually borne in the upper crown and staminate strobili on branchlets in the lower crown (Fowler and Roche 1977). Separation of male and female strobili within a crown is an important mechanism for preventing self-fertilization. Male flowers ripen and pollen is wind-disseminated in late May and early June at lower elevations and from mid-June to early July at higher elevations. Cones mature in August and early September the same year, and seeds ripen from late August to late September. Cones are shed during the fall and winter of the first year (Alexander 1958, 1965, Schmidt and Lotan 1980, USDA Forest Service 1974).

Seed Production

Although open-grown Engelmann spruce begin bearing cones when they are 4 to 5 feet tall and 15 to 40 years old, seed production does not become significant until trees are larger and older. The most abundant crops in natural stands are produced on healthy, vigorous, dominant trees 15 inches or more in diameter at breast height and 150 to 250 years old. Engelmann spruce is rated as a moderate to good seed producer (Alexander 1958, 1965, Alexander, et al. 1982, Hodson and Foster 1910, USDA Forest Service 1974). Good to bumper seed crops, based on the following criteria, are generally borne every 2 to 5 years, with some seed produced almost every year (Alexander and Noble 1976):

Number of sound seeds per acre	Seed crop rating
0–10,000	Failure
10,000–50,000	Poor
50,000–100,000	Fair
100,000–250,000	Good
250,000–500,000	Heavy
>500,000	Bumper

There is considerable variation in seed production from year to year and from area to area. In one study in Colorado covering 42 area-seed-crop years, 12 were rated good to bumper and 30 fair to failure (Noble and Ronco 1978). In another Colorado study covering 10 years and 13 locations, seed production was rated good or better in 6 years, and fair to failure in 4 years (Alexander et al. 1982). In an earlier study in Montana, 22 cone crops observed during a 45-year period west of the Continental Divide were rated as 5 good, 8 fair, and 9 poor. East of the Divide seed production was poorer; only 2 good and 4 fair years were reported for a 21-year period, while 15 were failures (Boe 1954). In other studies in Montana and the Intermountain Region, seed production was rated good to bumper in 1 year out of 5 with the other 4 years rated as failures (Roe 1967, Squillace 1954). Variability in seed quality accentuates differences in seed production. The proportion of sound seed is usually highest in years of highest seed production (Alexander et al. 1982).

Observations in spruce forests before seedfall have indicated that part of each seed crop is lost to cone and seed insects (Alexander 1974). In a recently completed study in Colorado, insect-caused loss in Engelmann spruce averaged 28% of the total seed produced during a 4-year period (1974–1977) (Schmid et al. 1981). The percentage of infested cones was highest during years of poor seed production. The primary seed-eating insects were a spruce seedworm (*Cydia youngana* Kearfott = (*Laspeyresia youngana*)) and an unidentified species of fly, possibly a *Hylemya*, found only in the larvel stage.

Some loss of seed results from cutting and storing of cones by pine squirrels (*Tamiasciurus hudsonicus fremonti* Audubon and Bachman), but the actual quantitative loss is unknown. After seed is shed, small mammals such as deer mice (*Peromyscus maniculatus* Wagner), red-backed mice (*Clethrionomys gapperi* Vigors), mountain voles (*Microtus montanus* Peale), and chipmunks (*Eutamias minimus* Bachman) are the principal source of seed loss. Undoubtedly mammals consume considerable seed, but the magnitude of losses is not known and results of studies on protecting seed are conflicting. For example, in western Montana spruce seedling success was little better on protected than unprotected seed spots (Schopmeyer and Helmers 1947), but in British Columbia, protection of spruce seed from rodents was essential to spruce regeneration success (Smith 1955).

Seed Dissemination

Most seed is shed by the end of October, although some falls throughout the winter. The small, winged seeds are light, averaging about 135,000 per pound (USDA Forest Service 1974). Practically all of the seed is disseminated by wind. Squirrels, other mammals, and birds are not important in seed dispersal.

Seed is dispersed long distances only in years of bumper seed crops. For example, studies in the Rocky Mountains show that 96,000 to 250,000 sound seeds per acre were dispersed 400 to 600 feet from the windward source into clearcut blocks 600 to 800 feet wide (Noble and Ronco 1978, Roe 1967). Seedfall in uncut stands ranged from 500,000 to 5,000,000 seeds per acre. In years of good to heavy seed crops—100,000 to 500,000 sound seeds per acre—seedfall into cleared openings diminished rapidly as distance from seed source increased. Prevailing winds influence the pattern of seedfall into openings 200 to 800 feet across. The amount of seed dispersed to the windward timber edge is about 80% of the seedfall under the uncut stand. About 40% of the amount of seedfall under uncut windward stands is dispersed as far as 100 feet (Alexander 1969, Alexander and Edminster 1983, Noble and Ronco 1978). Seedfall then diminishes steadily but at a less rapid rate of decline as distance increases to about two-thirds of the way—150 to 600 feet—across the openings. At those distances, the average number of seeds falling varies from about 25% (at 150 feet) to less than 5% (at 600 feet) of the number released in the uncut stand. Beyond this point, seedfall gradually increases toward the leeward timber edge, but is only about 30% of the seedfall along the windward edge (Alexander 1969, Alexander and Edminster 1983).

Seedling Development

Germination and Establishment.—Viability of Engelmann spruce seed is rated good and the vitality persistent. The average germinative capacity of spruce is higher than that of many associated species, as shown in the following tabulation (USDA Forest Service 1974).

Species	Average germinative capacity *percent*
Engelmann spruce	69
Subalpine fir	31–34
Lodgepole pine	65–80
Western white pine	44
Rocky Mtn. Douglas–fir	60–93
Western larch	57
Grand fir	46–57
Western hemlock	53–56
Pacific silver fir	20–26
White fir	30–37

Viable seeds of spruce that survive over winter normally germinate following snowmelt, when seedbeds are moist and air temperatures are at least 45° F. Field germination of spruce over long periods of time in Colorado has ranged from 0 to 28% of the sound seeds dispersed, depending upon the seedbed and environmental factors (Alexander 1984, Noble and Alexander 1977).

In the undisturbed forest, spruce seeds germinate and seedlings become established on duff, litter, partially decomposed humus, decaying wood, and mounds of mineral soil upturned by windthrown trees. Any disturbance that removes the overstory produces new microhabitats (Roe et al. 1970). Under these latter circumstances, germination and initial establishment is generally better on mineral soil and mixed mineral soil and humus seedbeds because moisture conditions are more stable (Alexander 1984, Boyd and Deitschman 1969, Day 1964, Noble and Alexander 1977, Roe and Schmidt 1964). Decayed wood, the natural forest floor, and undisturbed duff and litter are poor seedbeds because they dry out rapidly (Alexander 1984, Day 1964, Noble and Alexander 1977, Roe et al. 1970, Smith 1955). Spruce seedling establishment on burned seedbeds has been variable. Success is related to severity of burn, depth of ash, and amount of exposed mineral soil (Clark 1969, Roe et al. 1970, Shearer 1984). Once established (at least 3 years old), seedling ability to survive is not increased by a mineral soil seedbed, but is favored by adequate soil moisture, cool temperatures, and shade.

Engelmann spruce will germinate in all light intensities found in nature, but 40% to 60% of full shade is most favorable for seedling establishment at high elevations. Light intensity and solar radiation are high at elevations and latitudes where spruce grows in the central and southern Rocky Mountains, and seedlings do not establish readily in the open. Planted seedlings often develop a chlorotic appearance that has been attributed to solarization—a phenomenon by which light intensity inhibits photosynthesis and which ultimately results in death (Ronco 1970). Mortality can be reduced by shading seedlings. At lower elevations and higher latitudes in the northern Rocky Mountains, spruce can become established and survive in the open. Spruce can establish and survive better in lower light intensities than its common, intolerant associates such as lodgepole pine, Rocky Mountain Douglas-fir, and aspen, but at extremely low light intensities it cannot compete favorably with such shade-enduring associates as the true firs and hemlocks (Alexander 1958, 1965, Bates 1925).

Engelmann spruce is restricted to cold, humid habitats because of its low tolerance to high temperatures and drought (Bates 1923, Helmers et al. 1970). Solar radiation at high elevations heats soil surfaces up to 150° F and higher and increases water losses from both seedlings and soil by transpiration and evaporation (Alexander 1984, Noble and Alexander 1977, Roe et al. 1970).

Because of its slow initial root penetration and extreme sensitivity to heat in the succulent stage, drought- and heat-girdling cause substantial first-year spruce

seedling mortality (Alexander 1984, Day 1963, Noble and Alexander 1977).

Tree seedlings in the succulent stage are particularly susceptible to stem-girdling. The cortex is killed by a temperature of 130° F, but prolonged exposures to lower temperatures may also be lethal. On the Fraser Experimental Forest, heat-girdling was an important cause of early seedling mortality on unshaded seedbeds (Alexander 1984, Noble and Alexander 1977). Soil surface temperatures exceeded 150° F in the open on a north aspect and 160° on a south aspect at 10,500 feet elevation in the month of June. Maximum air temperature during this period did not exceed 78° F. In western Montana, at lower elevations, soil surface temperatures exceeded 160° F on gentle north slopes several times during one summer (Roe et al. 1970). Early shade protection improved survival of newly germinated spruce seedlings; 30% to 50% of the seedlings were lost to heat-girdling on unshaded plots, compared to 10% on shaded plots. Day (1963) studied heat and drought mortality of newly germinated spruce seedlings in southwestern Alberta, and found that when water was excluded nearly three-fourths of the mortality on four different unshaded seedbed types was caused by heat-girdling. Surface temperatures as low as 113° F caused heat girdling, but losses were not high until soil surface temperatures were above 122° F. Shading reduced heat-girdling on all seedbed types. Soil surface temperatures in excess of lethal levels for spruce seedlings, especially on burned seedbeds, have been reported in British Columbia (Smith 1955).

Air and soil temperatures (below the surface) are not usually directly responsible for seedling mortality, but they affect growth. Helmers et al. (1970) studied the growth of Engelmann spruce seedlings under 30 different combinations of day and night temperatures. They found that the greatest height and root growth, and top and root dry matter production was with a diurnal variation of 66° F (air and soil) day temperatures and 73° F (air and soil) night temperatures. Shepperd (1981), using the same night temperature regime, raised the day soil temperature to 73° F and significantly increased root growth.

Frost can occur any month of the growing season where spruce grows. It is most likely to occur in depressions and cleared openings because of cold air drainage and radiation cooling. Newly germinated spruce seedlings are most susceptible to early fall frosts. In a greenhouse and laboratory study, new seedlings did not survive temperatures as low as 15° F until about 10 weeks old (Noble 1973a). Terminal bud formation began at 8 weeks; buds were set and needles were mature at 10 to 12 weeks after germination.

After the first year, seedlings are most susceptible to frost early in the growing season when tissues are succulent. Shoots are killed or injured by mechanical damage resulting when tissue freezes and thaws. Frost damage has been recorded in most years in Colorado (Ronco 1967). In light frost years damage was minor, but heavy frosts either damaged or killed all new shoots of open-grown seedlings.

In the early fall, the combination of warm daytime temperatures, nighttime temperatures below freezing, and saturated soil unprotected by snow are conducive to frost-heaving. On the Fraser Experimental Forest, Colorado, these conditions generally occurred in about 1 out of 2 years (Alexander 1984, Noble and Alexander 1977). Frost-heaving has been one of the principal causes of first-year seedling mortality on scarified seedbeds on the north aspect (Alexander 1984). Furthermore, seedlings continue to frost-heave after four growing seasons. Shading has reduced losses by reducing radiation cooling.

The moisture condition of the seedbed during the growing season largely determines first-year seedling survival. On some sites in the central Rocky Mountains, summer drought is responsible for substantial first-year mortality, especially in years when precipitation is low or irregular. On the Fraser Experimental Forest in the central Rocky Mountains, drought and desiccation have caused more than half of the first-year seedling mortality on a south aspect, and nearly two-thirds of the total after 5 years (Alexander 1984). On a north aspect during the same period, drought has accounted for about 40% of first-year seedling mortality, and more than one-half of the mortality at the end of 5 years.

In the northern Rocky Mountains, late spring and early summer drought is a serious threat most years to first-year seedlings. In western Montana, all seedlings on one area were killed by drought in a 2-week period in late summer when their rate of root penetration could not keep pace with soil drying during a prolonged dry period (Roe et al. 1970). Late spring and early summer drought is also a serious cause of first-year seedling mortality in the southern Rockies. Drought losses can continue to be significant throughout the Rocky Mountains during the first 5 years of seedling development, especially during prolonged summer dry periods (Alexander 1984, Noble and Alexander 1977).

The moisture provided by precipitation during the growing season is particularly critical to seedling survival during the first year. Alexander and Noble (1971) studied the effects of amount and distribution of moisture on seedling survival in the greenhouse. Treatments simulated common summer precipitation patterns in north-central Colorado. They concluded that, under favorable seedbed and environmental conditions: (1) at least 1 inch of well-distributed precipitation is needed monthly before seedlings will survive drought; (2) with this precipitation pattern, more than 1.5 inches of monthly rainfall is not likely to increase seedling survival; but (3) few seedlings will survive drought with less than 2 inches of rainfall monthly when precipitation comes in only one or two storms.

Summer precipitation may not always benefit seedling survival and establishment. Summer storms in the Rocky Mountains may be so intense that much of the moisture runs off, especially from bare soil surfaces. Moreover, soil movement on unprotected seedbeds buries some seedlings and uncovers others (Roe et al. 1970).

Understory vegetation can be either a benefit or serious constraint to spruce seedling establishment (Alexander 1966, Day 1964, Ronco 1972). Spruce seedlings become established more readily on sites protected by willows (*Salix* spp.), shrubby cinquefoil (*Potentilla fruiticosa* L.), fireweed, and dwarf whortleberry than in the open. Because these plants compete less aggressively for available soil moisture than those listed below, the net effect of their shade is beneficial to seedling survival. In contrast, mortality occurs when spruce seedlings start near clumps of grass or sedges or scattered herbaceous plants such as mountain bluebells, currants (*Ribes* spp.), and Oregon grape that compete severely for moisture and smother seedlings with cured vegetation when compacted by snow cover.

The only significant biotic factor affecting spruce regenerating success on a long-term study on the Fraser Experimental Forest was birds. About 15% to 20% of the total mortality resulted from the clipping of cotyledons on newly germinated seedlings by grey-headed juncos (*Junco caniceps* Woodhouse) (Alexander 1984, Noble and Alexander 1977, Noble and Shepperd 1973).

Damping-off, needlecast, snowmold, insects, rodents, and trampling and browsing by large animals also kill spruce seedlings, but losses are no greater than for any other species (Alexander 1958, 1965).

The number of seeds required to produce a first-year seedling and an established seedling (at least 3 years old) and the number of first-year seedlings that produce an established seedling vary considerably, depending upon seed production, distance from source, seedbed, and other environmental conditions. In one study in clearcut openings in Colorado during the period 1961–1975, covering a wide variety of conditions, on the average 665 sound seeds (range 60–2,066) were required to produce a single first-year seedling, and 6,800 (range 926–20,809) to produce a seedling 4 or more years old. An average of 21 first-year seedlings was necessary to produce a single seedling 4 or more years old, although as few as 4 and as many as 24 first-year seedlings survived under different conditions (Noble and Ronco 1978).

Aspect and cultural treatments can also be important factors in the successful establishment of Engelmann spruce. In another Colorado study, an average of 18 sound seeds was required to produce a single first-year seedling on shaded, mineral soil seedbeds on a north aspect; and 32 sound seeds to produce a 5-year-old seedling. In contrast, 156 seeds were required to produce a first-year seedling on shaded, mineral soil seedbeds on a south aspect, and 341 seeds to produce a 5-year-old seedling (Alexander 1983, 1984). Shearer (1984) studying the effects of prescribed burning and wildfire after clearcutting on regeneration in the western larch type in Montana also found that natural and planted spruce survived better on the north aspect than on the south aspect.

Environmental conditions favorable and unfavorable to the establishment of Engelmann spruce natural regeneration are summarized in figure 4.

REGENERATION CONDITIONS

	FAVORABLE		UNFAVORABLE
a	>250,000 seed/acre	SEED CROP	<50,000 seed/acre
b	North and East	ASPECT	South and West
c	Ambient air >32°F night and <78°F day; maximum surface <90°F	TEMPERATURES	Ambient air <32°F night and >78°F day; maximum surface >90°F
d	>0.50 in. week	PRECIPITATION	<0.40 in. week
e	Light-textured, sandy-loam	SOIL	Heavy-textured, clay-loam
f	>40% exposed mineral soil	SEEDBED	<20% exposed mineral soil
g	50-70% dead shade		<30% dead shade
h	<2 in. duff and litter		>4 in. duff and litter
i	Light vegetative cover <30% non sod-forming		Heavy vegetative cover >60% sod-forming
j	Seedlings >12 weeks old by mid-Sept	SURVIVAL	Seedlings <12 weeks old by mid-Sept
k	Low population of birds and small mammals that eat tree seed and young seedlings		High population of birds and small mammals that eat tree seed and young seedlings
l	Protection from trampling		No protection from trampling
m	Fall snow cover when frost heaving conditions exist		No fall snow cover when frost heaving conditions exist
n	No late lying spring snowfields when conditions favorable to snowmold exist		Late lying spring snowfields when conditions favorable to snowmold exist

Figure 4.—Environmental conditions favorable and unfavorable to Engelmann spruce regeneration.

If trees are well distributed, stocking should not exceed about 600 to 800 stems per acre at age 30 years (Alexander and Edminster 1980, Edminster 1978). In order to obtain proper distribution and full utilization of the site however, at least 1,000 stems per acre should be established initially. This will allow for subsequent mortality and permit later thinning to obtain proper spacing and to select future crop trees.

Early Growth.—The early growth of Engelmann spruce is very slow (LeBarron and Jemison 1953). First-year spruce seedlings grown on mineral soil seedbeds under partial shade in Colorado have a rooting depth of 3 to 4 inches, with a total root length of 5 inches (Noble 1973b). In the Rocky Mountains of Arizona and New Mexico, root depths of vigorous one-year-old seedlings have been reported to average about 2.8 inches on shaded, mineral soil seedbeds, and on seedbeds where the depth of humus was about 1 inch (Jones 1971). Observations in the Rocky Mountains of Idaho and Montana, and in British Columbia indicate that first-year penetration of spruce seedlings averages only about 1.5 inches (Roe et al. 1970, Smith 1955).

Initial shoot growth of natural seedlings is equally slow in Colorado. First-year spruce seedlings are seldom over 1 inch tall. After 5 years, seedlings average 1 to 3 inches in height under natural conditions and 2 to 4 inches in height on both partially shaded and unshaded, prepared, mineral soil seedbeds. Seedlings 10 years old may be only 6 to 8 inches tall under natural conditions and 10 to 12 inches tall on both partially shaded and unshaded, mineral soil seedbeds[3] (fig. 5). After 10 years, trees grow at a more rapid rate, averaging about 4 to 5 feet in height in about 20 years in full sun or light overstory shade and, reaching about the same height after 40 years under moderate overstory shade. Severe suppression of seedling growth occurs at low light levels. It is not uncommon to find trees 100 years old and only 3 to 5 feet tall under the heavy shade of a closed forest canopy.

[3]Data on file RS-RM MFRWU 1252, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Figure 5.—Engelmann spruce seedlings on mineral soil seedbeds average only 8 to 12 inches in height after 10 years.

Seedling growth has been somewhat better elsewhere in the Rocky Mountains, especially at lower elevations and higher latitudes. For example, in one study in the Intermountain west, average annual shoot growth of natural 10-year-old seedlings averaged 4.5 inches on clearcut areas, and 3.2 inches on areas with a partial overstory (McCoughey and Schmidt 1982). Planted spruces, 5 to 8 years old, averaged 20 to 24 inches in height in Utah.[4] In Montana, planted spruces have been reported to reach breast height (4.5 feet) in about 10 years.[5]

Early diameter growth of Engelmann spruce is less affected by competition for growing space than that of its more intolerant associates. In a study of seed spot density in northern Idaho, diameter growth of spruce seedlings after 17 years was only slightly greater on thinned seed spots, and height growth was unaffected by the thinning. In contrast, diameter and height growth of western white pine increased significantly as the number of seedlings per seed spot decreased (Roe and Boe 1952).

Vegetative Reproduction

Engelmann spruce can reproduce by layering (Hodson and Foster 1910). It most often layers near timberline where the species assumes a dwarfed or prostrate form. Layering can also occur when only a few trees survive fires or other catastrophies. Once these survivors have increased to the point where their numbers alter the microenvironment to improve germination and establishment, layering diminishes. In general, this form of reproduction is insignificant in establishing and maintaining closed forest stands (Oosting and Reed 1952).

Sapling and Pole Stage to Maturity

Growth and Yield

Natural Stands.—Engelmann spruce is one of the largest of the high mountain species. Under favorable conditions, average stand diameter will vary from 15 to 30 inches and average dominant height from 45 to 130 feet, depending upon site quality and density[3] (fig. 6). Individual trees may exceed 40 inches in diameter and 160 feet in height (LeBarron and Jemison 1953). Engelmann spruce is a long-lived tree, maturing in about 300 years. Dominant spruces are often 250 to 450 years old, and trees 500 to 600 years old are not uncommon.

[4]Personal correspondence with Dr. Wyman C. Schmidt, Principal Silviculturist, FS-INT-RWU 1251, Intermountain Forest and Range Experiment Station, Bozeman, Mont.

[5]Personal correspondence with Mr. Orville Engelby, Assistant Director, Timber Management (silviculture), USDA Forest Service, R-4 Intermountain Region, Ogden, Utah.

Engelmann spruce has the capacity to make good growth at advanced ages. If given sufficient growing space, it will continue to grow steadily in diameter for 300 years, long after the growth of most associated trees species slows down (Alexander 1958, 1965, LeBarron and Jemison 1953).

Yields are usually expressed for the total stand. Engelmann spruce does not normally grow in pure stands but in varying mixtures with associated species. Average volumes per acre in old-growth (normally 250 to 350 years old) spruce-fir forests in the Rocky Mountains, may be practically nothing at timberline, 5,000 to 15,000 board feet on poor sites, and 25,000 to 40,000 board feet on better sites. Volumes as high as 80,000 to 100,000 board feet per acre have been reported for very old stands on exceptional sites (Pearson 1931, Thompson 1929). Average annual growth in virgin spruce-fir forests will vary from a net loss due to mortality to 80 to 200 board feet per acre, depending upon age, density, and vigor of the stand (Miller and Choate 1964). Engelmann spruce usually constitutes at least 70% and often more than 90% of the basal area in trees 5 inches d.b.h. and larger in these stands (Oosting and Reed 1952).

Figure 6.—Dominant Engelmann spruce on the Fraser Experimental Forest, Colorado. Tree is 18 inches in diameter, over 90 feet tall, and 250 years old at d.b.h.

Managed Stands.—With prompt restocking after timber harvest and periodic thinning to control stand density, growth of individual spruce trees and yields of spruce-fir stands can be greatly increased compared with unmanaged stands, and the time required to produce these volumes and sizes can be reduced. For example, in stands managed at the growing stock levels considered optimum for timber production (GSL 140 to 180) on 140- to 160-year rotations with a 20-year thinning interval, average volumes per acre will range from 30,000 to 40,000 board feet on poor sites to 90,000 to 105,000 board feet per acre on good sites (Alexander and Edminster 1980). Volume production substantially declines on all sites when growing stock level is reduced below the optimum for timber production, and the decline is greater with each successive reduction in GSL (table 2). Average annual growth will vary from 180 to 650 board feet per acre depending upon growing stock level, site quality, cutting cycle, and rotation age (Alexander and Edminster 1980). Moreover, since most subalpine fir will be removed in early thinnings, these yields will be largely from Engelmann spruce.

Rooting Habit

Engelmann spruce is considered to have a shallow root system. The weak tap root of seedlings does not persist beyond the juvenile stage, and when trees grow where the water table is near the surface or on soils underlain by impervious rock or clay hardpans, the weak, superficial lateral root system common to the seedling stage may persist to old age. Under these conditions, most roots are in the first 12 to 18 inches of soil. But where spruce grows on deep, porous, well-drained soils, the lateral root system may penetrate to a depth of 8 feet or more (Alexander 1958, 1965).

Reaction to Competition

Engelmann spruce is rated tolerant in its ability to endure shade (Baker 1949). It is definitely more shade-enduring than Rocky Mountain Douglas-fir, western white pine, lodgepole pine, aspen, western larch, or ponderosa pine but less so than subalpine fir (the most common associate throughout much of its range), grand fir, white fir, and mountain hemlock. Engelmann spruce is either a co-climax with subalpine fir or long-lived seral forest vegetation throughout much of its range. In the Rocky Mountains of British Columbia and Alberta, and south of Montana and Idaho, Engelmann spruce and subalpine fir occur as either codominants or in nearly pure stands of one or the other. In the Rocky Mountains of Montana and Idaho, and in Utah, eastern Oregon, and Washington, subalpine fir is the major climax species. Engelmann spruce may also occur as a major climax species, but more often it is a persistent long-lived seral species. Pure stands of either species can be found, however (Alexander 1980).

Although spruce-fir forests form climax or near-climax vegetation associations, they differ from most climax forests in that all stands are not truly all-aged

Table 2.—Estimated board-foot volume production per acre of spruce-fir in relation to growing stock level, site index, rotation age, and cutting cycle with a clearcut option (trees 8 inches d.b.h. and larger to a 6-inch top) (Alexander and Edminster 1980)

Rotation age	Cutting cycle	Growing stock level 40	60	80	100	120	140	160	180
----- years ----		-----------------------			thousand board feet			-----------------------	
					Site index 50				
100	20	7.1	8.9	10.4	11.6	12.0	11.7	11.4	10.9
120		9.2	12.1	14.6	16.4	17.4	17.8	17.4	16.2
140		11.2	14.8	18.1	21.0	22.8	23.7	23.9	23.1
160		13.3	17.9	21.8	25.3	27.8	29.4	30.9	29.9
100	30	7.5	9.1	10.5	11.4	11.6	11.4	11.0	10.3
120		10.0	12.7	15.1	16.8	17.5	17.4	17.2	16.1
140		12.2	15.7	18.8	21.1	23.1	23.5	23.5	22.5
160		14.6	19.0	22.7	26.4	28.6	29.8	30.2	28.8
					Site index 60				
100	20	9.1	12.0	14.1	16.1	17.0	17.4	17.6	17.0
120		11.6	15.6	19.2	21.8	23.6	25.2	26.2	25.8
140		14.1	19.3	23.8	27.2	29.7	31.6	33.3	34.3
160		16.6	22.9	28.3	32.6	36.0	39.2	41.3	42.4
100	30	9.8	12.5	14.3	15.6	16.5	17.0	17.0	16.3
120		12.8	17.0	20.4	22.6	24.0	25.4	26.2	25.2
140		15.4	20.6	25.1	28.6	31.5	33.7	34.9	33.7
160		18.1	24.2	29.1	33.9	37.9	40.8	42.4	41.4
					Site index 70				
100	20	11.7	15.0	17.9	20.6	23.0	24.7	25.4	24.9
120		14.8	19.2	23.6	27.6	31.2	34.1	36.1	35.8
140		17.6	23.8	29.1	34.3	38.9	42.7	45.1	46.2
160		20.6	27.7	34.2	40.6	46.6	50.7	54.2	56.8
100	30	12.4	16.2	19.2	21.6	23.2	24.3	24.6	24.1
120		16.1	21.7	26.0	29.6	32.8	34.8	25.5	34.8
140		19.0	25.5	31.6	36.9	40.7	43.4	44.7	45.1
160		22.1	29.8	37.1	43.0	48.2	52.3	54.9	56.5
					Site index 80				
100	20	13.8	18.2	22.2	26.0	29.6	32.5	34.3	34.1
120		17.4	23.9	29.4	34.2	38.6	43.7	46.4	47.4
140		20.7	28.8	35.7	41.6	47.5	52.9	57.0	60.1
160		24.3	33.4	41.8	49.0	56.0	62.6	68.2	72.6
100	30	15.5	20.0	24.2	27.8	30.6	30.4	33.5	33.0
120		19.8	25.7	31.8	37.4	41.8	45.0	46.4	45.7
140		23.2	31.4	38.1	44.8	50.1	54.6	57.8	58.5
160		27.0	33.3	45.6	53.6	60.2	65.9	69.8	71.2
					Site index 90				
100	20	16.4	22.6	27.8	32.1	35.9	39.1	42.5	44.5
120		20.4	28.6	35.4	41.3	46.9	52.0	56.2	59.9
140		24.2	33.9	42.3	50.1	57.4	63.7	69.3	74.2
160		28.2	39.4	49.4	58.7	67.2	74.7	82.2	89.0
100	30	18.7	25.2	20.7	35.5	39.3	42.2	43.8	43.2
120		23.5	31.9	39.7	46.6	52.2	56.4	58.9	58.2
140		27.4	37.2	46.9	55.6	62.6	68.3	72.1	73.1
160		31.7	43.2	54.4	65.0	73.6	80.6	85.8	87.0
					Site index 100				
100	20	19.6	26.6	32.7	38.4	43.6	48.2	51.8	54.2
120		24.2	33.2	41.5	49.0	56.0	62.4	68.0	71.6
140		28.6	39.5	49.8	59.2	68.0	76.0	83.2	88.1
160		33.1	45.8	57.8	68.5	79.4	88.8	97.6	104.6
100	30	21.9	29.2	36.3	43.3	48.7	52.6	54.2	53.6
120		27.6	37.9	47.6	56.3	63.2	69.2	72.1	71.4
140		32.1	44.4	56.0	66.4	75.3	82.7	87.4	88.9
160		36.6	51.2	64.5	76.5	87.7	96.6	103.0	104.8

(LeBarron and Jemison 1953). Some stands are clearly single-storied, indicating that desirable spruce forests can be grown under even-aged management. Other stands are two- or three-storied, and multistoried stands are not uncommon (Alexander 1974). These may be the result of either past disturbances such as fire, insect epidemics, or cutting, or the gradual deterioration of old-growth stands associated with normal mortality from wind, insects, and diseases. The latter circumstance is especially evident in the formation of some multistoried stands. On the other hand, some multistoried stands appear to have originated as uneven-aged stands and are successfully perpetuating this age-class structure (Hanley et al. 1975).

Climax forests are not easily displaced by other vegetation, but fire, logging, and insects have played an important part in the successional status and composition of spruce-fir forests. Complete removal of the stand by fire or logging results in such drastic environmental changes that spruce and fir are usually replaced by lodgepole pine, aspen, or shrub and grass communities (Roe et al. 1970, Stahelin 1943). The kind of vegetation initially occupying the site usually determines the length of time it takes to return to a spruce-fir forest. It may vary from a few years if the site is initially occupied by lodgepole pine or aspen to as many as 300 years if grass is the replacement community (fig. 7).

The ecophysiology of Engelmann spruce in relation to its common associates is becoming better understood. Kaufmann (1975, 1976, 1979, 1982a, 1982b, 1984a, 1984b), Kaufmann and Troendle (1981), and Kaufmann et al. (1982) summarized what is known about the utilization of water by Engelmann spruce as follows: (1) leaf water potential decreases in proportion to the transpiration rate but is influenced by soil temperature and water supply; (2) needle water vapor conductance (directly proportional to stomatal opening) is controlled primarily by visible irradiance and absolute humidity difference from needle to air (evaporative demand), with secondary effects from temperature and water stress; (3) nighttime minimum temperatures below 39° F retard stomatal opening the next day, but stomata function well from early spring to late fall, and high transpiration rates occur even with considerable snowpack on the ground; (4) leaf water vapor conductance is higher in Engelmann spruce than in subalpine fir, but lower than in lodgepole pine or aspen; (5) Engelmann spruce trees have less total needle area per unit area of sapwood water conducting tissue than subalpine fir but more than lodgepole pine or aspen; and (6) Engelmann spruce trees have a greater needle area per unit of bole or stand basal area than subalpine fir, lodgepole pine, or aspen. At equal basal area, annual canopy transpiration of spruce is about 80% greater than lodgepole pine, 50% greater than subalpine fir, and 220% greater than aspen. These high rates of transpiration cause Engelmann spruce to occur primarily on the wetter sites.

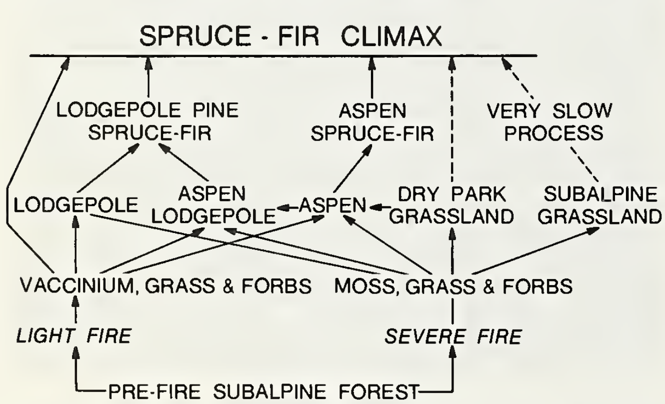

Figure 7.—Natural succession in Rocky Mountain subalpine spruce-fir forests after fire.

Silvicultural Systems and Cutting Methods

Both even- and uneven-aged silvicultural systems are appropriate for use in Engelmann spruce forests, but not all cutting methods under each system are applicable in every stand nor will every cutting method meet specific management objectives (Alexander 1977, Alexander and Engelby 1983). The even-aged cutting methods include clearcutting, which removes all trees in strips, patches, blocks, or stands with a single cut (fig. 8); and shelterwood cutting, which removes trees in one, two or three cuts (fig. 9) and its modifications. Because of susceptibility to windthrow, the seed-tree method is not a suitable way to regenerate spruce. The seedbed is prepared for regeneration after clearcutting, or after the seed cut with shelterwood cutting, by various methods ranging from burning and mechanical scarification, to only that associated with logging activity (Alexander 1974, Alexander and Engelby 1983).

The uneven-aged cutting methods appropriate to spruce are individual tree and group selection cuttings (fig. 10) and their modifications, which remove selected trees in all size classes at periodic intervals over the entire area or in groups up to 2 acres in size. Reproduction occurs continuously, but methods of site preparation are limited.

Shelterwood and individual tree selection cutting methods will favor associated species such as true firs and hemlocks over spruce. Clearcutting and group selection cutting methods will favor Engelmann spruce over these more tolerant associates but will increase the proportion of intolerant associates like lodgepole pine and Douglas-fir.

Damaging Agents

Windfall.—Engelmann spruce is susceptible to windthrow, especially after any kind of initial cutting in old-growth forests (fig. 11). Partial cutting increases the risk because the entire stand is opened up and therefore vulnerable. Windfall is usually less around clearcuts because only the boundaries between cut and leave areas are vulnerable, but losses can be substantial if no special effort is made to locate windfirm cutting unit boundaries (Alexander 1964, 1967). While the tendency of spruce to windthrow is usually attributed to a shallow

root system, the development of the root system varies with soil and stand conditions. Trees that have developed together in dense stands over long periods of time mutually protect each other and do not have the roots, boles, or crowns to withstand sudden exposure to wind if opened up too drastically. If the roots and boles are defective, the risk of windthrow is increased. Furthermore, regardless of the kind or intensity of cutting, or soil and stand conditions, windthrow is greater on some exposures than others. Alexander (1974) has identified spruce windfall risk in relation to exposures in Colorado as follows:

Below Average
1. Valley bottoms, except where parallel to the direction of prevailing winds, and flat areas.
2. All lower, and gentle, middle north- and east-facing slopes.
3. All lower, and gentle, middle south- and west-facing slopes that are protected from the wind by considerably higher ground not far to windward.

Above Average
1. Valley bottoms parallel to the direction of prevailing winds.

Figure 8.—Clearcutting old-growth spruce-fir in alternate strips on the Fraser Experimental Forest, Colorado.

Figure 9.—First cut of a two-step shelterwood in old-growth spruce-fir on the Fraser Experimental Forest, Colorado.

Figure 10.—Group selection cutting in old-growth spruce-fir on the Fraser Experimental Forest, Colorado.

Figure 11.—Windthrown Engelmann spruce, Fraser Experimental Forest, Colorado.

2. Gentle, middle south and west slopes not protected to the windward.
3. Moderate to steep middle, and all upper north- and east-facing slopes.
4. Moderate to steep middle south- and west-facing slopes protected by considerably higher ground not far to windward.

Very High
1. Ridgetops.
2. Saddles in ridges.
3. Moderate to steep middle south- and west-facing slopes not protected to the windward.
4. All upper south- and west-facing slopes.

The risk of windfall is increased at least one category by such factors as poor drainage, shallow soils, defective roots and boles, and overly dense stands. Conversely, the risk of windfall is reduced if the stand is open-grown or composed of young, vigorous, sound trees. All situations become very high risk if exposed to special topographic situations such as gaps or saddles in ridges at higher elevations to the windward that can funnel winds into the area (Alexander 1964, 1967, 1974).

Insects.—The spruce beetle (*Dendroctonus rufipennis* Kirby) is the most serious insect pest of Engelmann spruce (Schmid and Frye 1977). It is restricted largely to mature and overmature spruce, and epidemics have occurred throughout recorded history. One of the most damaging recorded outbreaks was in Colorado from 1939 to 1951, when beetles killed nearly 4 billion board feet of standing spruce (Massey and Wygant 1954). Outbreaks have been largely associated with extensive windthrow, where down trees have provided an ample food supply needed for a rapid buildup of beetle populations. Cull material left after logging has also started outbreaks, and there are examples of heavy spruce beetle populations developing in scattered trees windthrown after heavy partial cutting. The beetle progeny then emerge to attack living trees, sometimes seriously damaging the residual stand. Occasionally, heavy spruce beetle outbreaks have developed in overmature stands with no recent history of cutting or windfall, but losses in uncut stands that have not been subjected to catastrophic wind storms have usually been no greater than normal mortality in old growth (Alexander 1974). Engelmann spruce is attacked by other insects, but only the defoliating western spruce budworm (*Choristoneura occidentalis* Freeman) is potentially dangerous (Furniss and Carolin 1977).

Diseases.—The most common diseases of Engelmann spruce are caused by wood-rotting fungi that result in loss of volume and predispose trees to windthrow and windbreak (Hinds and Hawksworth 1966). In a recent study of cull indicators and associated decay in Colorado, the major root and butt fungi in mature to overmature Engelmann spruce were identified as *Phellinus nigrolimitatus* (Rohm.) Bourd. et Galz., *Flammula alnicola* (Fr.) Kummer, *Polyporus tomentosus* var. *circnatus* (Fr.) Sartory et. Maire, *Gloeocystidiellum radiosum* (Fr.) Bord., and *Coniophora puteana* (Schum. ex Fr.) Karst. Trunk rots, which caused 88% of the decay, were associated with *Phellinus pini* (Thore ex Fr.) Pilat, *Haematosterceum sanguinolentum* (Alb. ex Schw. ex Fr.) Pouz., *Echinodontium sulcatum* (Burt) Gross, and *Amylosterceum chailletii* (Pers ex Fr.) Boid. Spruce broom rust (*Chrysomyxa arctostaphyli* Diet.) is also common in spruce-fir forests. It causes bole deformation, loss of volume, and spiketops; increases susceptibility to windbreak; and provides infection courts for decay fungi in spruce (Alexander 1958, 1965, Hinds and Hawksworth 1966). Dwarfmistletoe (*Arceuthobium microcarpum* (Engelm.) Hawks. and Wiens) causes heavy mortality in spruce in Arizona and New Mexico, but it has a limited range in the Southwest and is not found in the central Rocky Mountains (Hawksworth and Wiens 1972).

Fire.—Thin bark and persistence of dead lower limbs make Engelmann spruce susceptible to destruction or severe injury by fire. Many root and trunk rots in old growth appear to be associated with fire injury. Because of the climate where spruce grows, the risk of fire is less than in warmer and drier climates (Alexander 1958, 1965).

PROPERTIES AND USES OF THE WOOD

Engelmann spruce is one of the lightest of the important commercial woods in the United States. The wood is generally straight grained, has moderately small shrinkage, can be readily air-dried, and is a uniform color (McSwain et al. 1970). It is rated low in beam and post strength and in shock resistance. The wood is soft and machines well for ordinary uses. It has good nail-holding properties, glues well, and is easy to work, but paint-holding properties are only average. If sufficient time is allowed, the lumber can be kiln-dried without difficulty. The heartwood and sapwood are not durable when used under conditions favorable to decay. Spruce is considered somewhat resistant to preservative treatment; however, crossties have been successfully pressure-treated for many years (Anderson 1956).

The lumber of spruce is likely to contain many small knots. Consequently, it yields only minor amounts of select grades of lumber, but a relatively high proportion in the common grades (Mueller and Barger 1963). In the past, spruce was used principally for mine timbers, railroad ties, and poles. Today much of the lumber of spruce is used in home construction where high strength is not required and for prefabricated wood products. In recent years, rotary-cut spruce veneer has been used in plywood manufacture. Other uses of spruce include specialty items such as violins and pianos and in aircraft construction (McSwain et al. 1970). Spruce has not been used much for pulp and paper, but its pulping properties are excellent. Long fibers, light color, and absence of resins permit it to be pulped readily by the sulfite, sulfate, or groundwood processes (Anderson 1956).

GENETICS

Population Differences

Available information on population differences of Engelmann spruce is limited to relatively few studies. For example, spruce from high elevation seed sources and northern latitudes break dormancy first in the spring and are the first to become dormant in the fall when grown in low elevation nurseries with low and middle elevation seed sources. Conversely, low elevation and southern latitude seed sources frequently are more resistant to spring frosts, but are less winterhardy than middle and high elevation seed sources (Fowler and Roche 1977). In one study that compared seedlings from 20 seed sources, ranging from British Columbia to New Mexico, planted at an elevation of 9,600 feet in Colorado, seedlings from northern latitudes and lower elevations made the best height growth (Shepperd et al. 1981). Overall survival from all sources was 73%, with no significant differences between sources.

Races and Hybrids

There are no recognized races or geographical varieties of Engelmann spruce (Little 1979). There is

abundant evidence that natural introgressive hybridization between Engelmann and white spruce occurs in sympatric areas, especially around Glacier Park in Montana (Daubenmire 1974). It has been suggested that Engelmann and Sitka spruces (*Picea sitchensis* (Bong.) Carr) cross in British Columbia, but it seems more likely that the crosses are between Sitka and white spruce. Engelmann spruce has been artifically crossed with several other spruces, but with only limited success (Fowler and Roche 1977).

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APPENDIX

Habitat types, community types and plant communities in which *Picea engelmannii* is a major climax, co-climax, minor climax, or major seral

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
			Picea engelmannii series			
Picea engelmannii / Acer glabrum H.T.	Chiricahua Mountains, Arizona; Sacramento Mountains, New Mexico	Warm moist	Climax	*Abies Lasiocarpa* *Pseudotsuga menziesii* *Populus tremuloides*	*A. glabrum* *Bromus ciliatus* *Viola canadensis* *Smilacina stellata*	Alexander et al. 1984a Moir and Ludwig 1979
Picea engelmannii / Juniperus communis H.T.	Wind River and Absaroka Mountains, northwestern Wyoming	Warm dry	Climax	*Pinus flexilis* *P. menziesii* *Pinus albicaulis* *Pinus contorta*	*J. communis* *Arnica cordifolia* *Frasera speciosa*	Steele et al. 1983
Picea engelmannii / Linnaea borealis H.T.	Mountains of Montana east of Continental Divide; Wind River Mountains, northwestern Wyoming	Cool well-drained	Climax	*P. contorta* *P. menziesii*	*L. borealis* *Vaccinium globulare* *Symphoricarpos albus* *J. communis*	Pfister et al. 1977 Steele et al. 1983
Picea engelmannii / Physocarpus malvaceus H.T.	Mountains of south-central Montana, eastern Idaho, and northwestern Wyoming	Warm moist	Climax	*A. lasiocarpa* (minor climax) *P. contorta* *P. menziesii*	*P. malvaceus* *Galium triflorum* *S. albus* *Spiraea betulifolia*	Pfister et al. 1977 Steele et al. 1983
Picea engelmannii / Ribes montigenum H.T.	Wind River Mountains, northwestern Wyoming; mountains of southern Utah	Cool dry to well-drained	Climax	*P. contorta* *P. menziesii* *P. albicaulis* *P. tremuloides*	*R. montigenum* *Aquilegia caerulea* *Sibbaldia procumbens* *Arnica latifolia* *Astragalus miser*	Pfister 1972 Steele et al. 1983 Youngblood 1984[1]
Picea engelmannii / Vaccinium caespitosum H.T.	Mountains of northwestern Montana and northern Utah	Cool well-drained	Climax	*Larix occidentalis* *Pinus ponderosa* *P. menziesii* *P. contorta*	*V. caespitosum* *L. borealis* *Vaccinium scoparium* *Calamagrostis rubescens* *R. montigenum*	Mauk and Henderson 1984 Pfister et al. 1977
Picea engelmannii / Vaccinium myrtillus H.T. *P. engelmannii / V. myrtillus-Polemonium pulcherrimum* H.T. [*P. engelmannii / V. scoparium-P. delicatum* H.T.]	Mountains of southern Colorado and northern New Mexico	Cool dry	Climax	*A. lasiocarpa* (minor climax) *Pinus aristata* *P. tremuloides*	*P. delicatum* (*P. pulcherrimum*) *Senecio* spp. *Deschampsia caespitosa* *Poa reflexa*	DeVelice et al. 1984[2] Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Picea engelmannii / Vaccinium scoparium H.T.	Wind River and Bighorn Mountains, Wyoming; mountains of northern Utah	Cool dry	Climax	*A. lasiocarpa* (minor climax WR Mts) *P. flexilis* *P. contorta* *P. menziesii* *P. albicaulis*	*V. scoparium* *A. cordifolia* *Carex rossii* *Antennaria* spp. *Fragaria virginiana*	Hoffman and Alexander 1976 Mauk and Henderson 1984 Steele et al. 1983
Picea engelmannii / Bromus ciliatus H.T.	Mogollon and Black Mountains, New Mexico	Cool dry	Climax	*P. menziesii*	*B. ciliatus* *C. rossii* *A. miser* *Fragaria* spp.	Fitzhugh et al. 1984[3]
Picea engelmannii / Elymus triticoides H.T.	Capitan Mountains, New Mexico	Cool dry to well-drained	Climax or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii*	*E. triticoides* *A. glabrum* *Jamesia americana*	Alexander et al. 1984a Moir and Ludwig 1979

Habitat type, community type or plant community	Location	Site	Successional status P. engelmannii	Principal tree associates	Principal understory species	Authority[1]
Picea engelmannii / *Carex disperma* H.T.	Mountains of central and southern Idaho, and northwestern Wyoming	Cool moist	Climax	*A. lasiocarpa* *P. contorta* *Picea pungens*	*C. disperma* *Pyrola secunda* *G. triflorum*	Steele et al. 1981 Steele et al. 1983
Picea engelmannii / *Carex foenea* H.T.	Pinaleno Mountains, Arizona	Cool dry	Climax	Generally in pure stands	*C. foenea*	Moir and Ludwig 1979
Picea engelmannii / *Arnica cordifolia* H.T.	Mountains of northwestern Wyoming	Cool well-drained	Climax	*P. menziesii* *P. flexilis* *P. albicaulis* *P. tremuloides*	*A. cordifolia* *C. rossii* *A. miser* *F. speciosa*	Steele et al. 1983
Picea engelmannii / *Caltha leptosepala* H.T.	Uinta Mountains, Utah; mountains of northwestern Wyoming and Idaho	Cool moist	Climax	*A. lasiocarpa* *P. contorta*	*C. leptosepala* *V. scoparium* *D. caespitosa*	Mauk and Henderson 1984 Steele et al. 1983
Picea engelmannii / *Clintonia uniflora* H.T.	Mountains of northwestern Montana	Warm moist to dry	Climax	*P. contorta* *P. ponderosa* *P. menziesii* *L. occidantalis*	*C. uniflora* *V. caespitosum* *Aralia nudicaulis* *Cornus canadensis*	Pfister et al. 1977
Picea engelmannii / *Equisetum arvense* H.T.	Mountains of north-central Washington, Montana, central Idaho, northwestern Wyoming, and northern Utah	Warm to cool wet	Climax	*A. lasiocarpa* *P. contorta* *P. pungens*	*E. arvense* *Equisetum seirpoides* *Streptopus amplexifolius* *Senecio triangularis* *Luzula parviflora*	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Williams and Lillybridge 1983
Picea engelmannii / *Galium triflorum* H.T.	Mountains of south-central Montana, central Idaho, and north-western Wyoming	Warm moist	Climax	*A. lasiocarpa* *P. contorta* *P. pungens* *P. ponderosa* *P. menziesii*	*G. triflorum* *Actaea rubra* *S. stellata* *S. amplexifolius*	Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
Picea engelmannii / *Geum rossii* H.T.	San Francisco Peaks, Arizona	Cool dry	Climax	*P. tremuloides*	*G. rossii* *P. delicatum* *Festuca brachyphylla*	Moir and Ludwig 1979
Picea engelmannii / *Hypnum revolutum* H.T.	Mountains of southeastern Idaho and north-western Wyoming	Cool dry	Climax	*P. flexilis* *P. albicaulis* *P. menziesii*	*H. revolutum* *Discranowiesia crispula*	Steele et al. 1981 Steele et al. 1983
Picea engelmannii / *Senecio cardamine* H.T.	Blue Mountains, Arizona	Cool moist	Climax	*A. lasiocarpa* *P. menziesii* *P. ponderosa* *Pinus strobiformis* *Abies concolor* *P. tremuloides*	*S. cardamine* *Geranium richardsonii* *Fragaria ovalis* *V. canadensis*	Fitzhugh et al. 1984[3]
Picea engelmannii / *Senecio streptanthifolius* H.T.	Mountains of central and southwestern Montana	Cool dry to well-drained	Climax	*P. flexilis* *P. albicaulis* *P. menziesii* *P. contorta*	*S. streptanthifolius* *P. secunda* *A. cordifolia*	Pfister et al. 1977
Picea engelmannii / *Smilacina stellata* H.T.	Mountains of Montana east of Continental Divide	Warm moist	Climax	*P. contorta* *P. ponderosa* *P. menziesii*	*S. stellata* *Smilacina racemosa* *Thalictrum occidentale*	Pfister et al. 1977

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Picea engelmannii / *Trifolium dasyphyllum* H.T.	High mountains of central Colorado	Cold dry	Climax or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides* *P. flexilis*	*T. dasyphyllum* *Pyrola chlorantha* *Sedum lanceolatum* *Trisetum spicatum*	Hess 1981
Picea engelmannii / Moss spp. H.T.	Mountains of New Mexico and Arizona	Cool moist to well-drained	Climax or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides* *P. aristata* *P. menziesii*	Moss spp. *Ribes* spp. *Lathyrus arizonicus* *Vaccinium* spp. *Rosa* spp.	Alexander et al. 1984b[4] Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Picea engelmannii / Bottomlands P.C.	Mountains of central Oregon	Warm moist	Long-lived seral to *Abies amabilis*	*A. amabilis* *P. menziesii* *P. contorta* *P. ponderosa*	*L. borealis* *Rubus ursinus*	Volland 1976
Picea engelmannii / Scree H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Climax	*A. lasiocarpa* (minor climax)	*J. communis* *Saxifraga bronchialis*	DeVelice et al. 1984[2]
			Abies lasiocarpa series			
Abies lasiocarpa / *Acer glabrum* H.T.	Mountains of of central and southern Idaho, northern and central Utah, and northwestern Wyoming; mountains of northern New Mexico	Warm moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides* *P. pungens* *A. concolor*	*A. glabrum* *T. occidentale* *Thalictrum fendleri* *Osmorhiza chilensis* *A. cordifolia*	Alexander et al. 1984b[4] Mauk and Henderson 1984 Steele et al. 1981 Steele et al. 1983 Youngblood 1984[1]
Abies lasiocarpa / *Alnus sinuata* H.T.	Mountains of central Idaho and central and south-western Montana	Cool moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *L. occidentalis*	*A. sinuata* *V. scoparium* *Xerophyllum tenax* *V. globulare*	Pfister et al. 1977 Steele et al. 1981
Abies lasiocarpa / *Berberis repens* H.T.	Mountains of Utah, north-western Wyoming, and southeastern Idaho	Warm to cool, well-drained	Minor climax to *A. lasiocarpa*	*A. lasiocarpa* P. pungens *P. contorta* *P. menziesii* *P. flexilis* *A. concolor* *P. tremuloides*	*B. repens* R. montigenum *Carex geyeri* *Pachistima myrsinites* *Symphoricarpos oreophilus*	Mauk and Henderson 1984 Pfister 1972 Steele et al. 1983 Youngblood 1984[1]
Abies lasiocarpa / *Clematis pseudoalpina* H.T.	Mountains of Montana east of Continental Divide	Warm dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. flexilis* *P. contorta* *P. menziesii*	*C. pseudoalpina* *Clematis tenuiloba*	Pfister et al. 1977
Abies lasiocarpa / *Juniperus communis* H.T.	Mountains of central Idaho, northwestern Wyoming, Utah, northern Arizona, and New Mexico	Warm to cold dry	Seral to or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides* *A. concolor* (AZ, NM only) *P. pungens* (UT)	*J. communis* *P. secunda* *Shepherdia canadensis* *V. globulare* *Rosa woodsii* *S. oreophilus*	Mauk and Henderson 1984 Moir and Ludwig 1979 Steele et al. 1981 Steele et al. 1983 Youngblood 1984[1]

Habitat type, community type or plant community	Location	Site	Successional status P. engelmannii	Principal tree associates	Principal understory species	Authority[1]
Abies lasiocarpa / Linnaea borealis H.T. *A. lasiocarpa-Picea engelmannii / L. borealis* P.C.	Mountains of north-central Washington, Montana, central and southern Idaho, northwestern Wyoming and central Colorado	Cool, moist to well-drained	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. tremuloides* *A. concolor* *L. occidentalis*	*L. borealis* *A. cordifolia* *V. scoparium* *C. rubescens* *Rubus parviflorus*	Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974[5] Williams and Lillybridge 1983
Abies lasiocarpa / Menziesia ferruginea H.T.	Mountains of southeastern Washington, eastern Oregon, Montana, Idaho, and northwestern Wyoming	Cool moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *Pinus monticola* *L. occidentalis*	*M. ferruginea* *V. globulare* *Rhododendron albiflorum* *Ledum glandulosum* *A. latifolia* *X. tenax*	Cooper et al. 1983[6] Daubenmire and Daubenmire 1968 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa / Oplopanax horridum H.T.	Mountains of northern to wet Montana	Cool moist	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. monticola* *P. menziesii* *L. occidentalis*	*O. horridum* *Taxus brevifolia*	Pfister et al. 1977
Abies lasiocarpa / Pachistima myrsinites H.T. *A. lasiocarpa-Picea engelmannii / P. myrsinites* P.C.	Mountains of southern British Columbia and north-central Washington; Rocky Mountains of Canada south to southern Colorado	Warm dry to well-drained	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. monticola* *P. tremuloides* *L. occidentalis*	*P. myrsinites* *C. uniflora* *G. triflorum* *C. geyeri* *Erigeron* spp.	Daubenmire and Daubenmire 1968 Hess and Wasser 1982[8] McLean 1970 Steen and Dix 1974[5] Williams and Lillybridge 1983
Abies lasiocarpa / Phyllodoce emptriformis P.C.	Eastside Cascades, north-central Washington	Cool moist	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. albicaulis*	*P. emptriformis* *V. scoparium*	Williams and Lillybridge 1983
Abies lasiocarpa / Physocarpus malvaceus H.T.	Mountains of eastern Idaho, northwestern Wyoming, and northern and central Utah	Warm moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides*	*P. malvaceus* *A. cordifolia* *Amelanchier alnifolia* *Sorbus scopulina* *A. glabrum* *S. canadensis*	Mauk and Henderson 1984 Steele et al. 1983 Youngblood 1984[1]
Abies lasiocarpa / Rhododendron albiflorum P.C.	Eastside Cascades, north-central Washington	Cool moist	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta*	*R albiflorum* *L glandulosum*	Williams and Lillybridge 1983
Abies lasiocarpa / Ribes montigenum H.T.	Mountains of southern Montana, idaho, Utah, and northwestern Wyoming	Cool dry	Seral to or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*R. montigenum* *A. latifolia* *T. fendleri* *Antennaria microphylla* *Mertensia arizonica*	Mauk and Henderson 1984 Pfister 1972 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Youngblood 1984[1]

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies lasiocarpa / *Rubus parviflorus* H.T.	Mimbres and Mogollon Mountains, New Mexico; San Juan Mountains, Colorado	Cool moist	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *A. concolor* *P. tremuloides*	*R. parviflorus* *Vaccinium myrtillus* *A. glabrum*	DeVelice et al. 1984[2] Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Abies lasiocarpa / *Salix glauca* H.T. *A. lasiocarpa-Picea engelmannii* / *S. glauca* H.T.	High mountains of Colorado	Cold wet	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. flexilis*	*S. glauca* *V. myrtillus* *P. pulcherrimum* *Acomastylis rossii*	Hess 1981 Hess and Wasser 1982[6] Komarkova 1984[8]
Abies lasiocarpa / *Shepherdia canadensis* H.T. *A. lasiocarpa-Picea engelmannii* / *S. canadensis* P.C.	Bighorn Mountains, north-central Wyoming; mountains of north-central Colorado	Cool to warm dry	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides*	*S. canadensis* *V. scoparium*	Hoffman and Alexander 1976 Steen and Dix 1974[5]
Abies lasiocarpa / *Spiraea betulifolia* H.T.	Mountains of central and southern Idaho, and northwestern Wyoming	Warm dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. albicaulis*	*S. betulifolia* *C. geyeri* *C. rubescens* *P. myrsinites*	Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa / *Symphoricarpos albus* H.T.	Mountains of southeastern Idaho and northwestern Wyoming	Warm well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. tremuloides*	*S. albus* *A. alnifolia* *C. rubescens*	Steele et al. 1983
Abies lasiocarpa / *Vaccinium caespitosum* H.T.	Mountains of south central Montana, central Idaho, and northern and central Utah	Cool well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*V. caespitosum* *L. borealis* *C. rubescens* *V. scoparium* *A. cordifolia*	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Youngblood 1984[1]
Abies lasiocarpa / *Vaccinium globulare* H.T.	Mountains of Montana, central and southern Idaho, northern Utah, and northwestern Wyoming	Cool well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. tremuloides*	*V. globulare* *P. myrsinites* *Lonicera utahensis* *A. cordifolia*	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa / *Vaccinium membranaceum* H.T.	Blue Mountains, Washington and Oregon; mountains of central Utah	Warm dry to well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. tremuloides* *L. occidentalis*	*V. membranaceum* *P. myrsinites* *A. cordifolia* *C. rossii*	Hall 1973 Youngblood 1984[1]
Abies lasiocarpa / *Vaccinium myrtillus* H.T. [*A. lasiocarpa* / *V. myrtillus-Linnaea borealis* H.T.] [*A. lasiocarpa* / *V. myrtillus-Rubus parvilorus* H.T.] [*A. lasiocarpa* / *Vaccinium scoparium-L. borealis* H.T.]	Mountains of eastern Arizona, northern New Mexico, and southern Colorado; La Sal mountains, Utah	Cool well-drained	Climax or co-climax with *A. lasiocarpa* (AZ)	*A. lasiocarpa* *A. concolor* *P. menziesii* *P. tremuloides* *P. aristata* *P. flexilis*	*V. myrtillus* *V. scoparium* *Lonicera involucrata* *P. myrsinites* *A. cordifolia* *R. montigenum* *L. borealis* *R. parviflorus*	Alexander et al. 1984b[4] DeVelice et al. 1984[2] Fitzhugh et al. 1984[3] Moir and Ludwig 1979 Youngblood 1984[1]

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies lasiocarpa / Vaccinium scoparium H.T. *A. lasiocarpa-Picea engelmannii / V. scoparium* H.T.; P.C. [*P. engelmannii / V. scoparium* H.T.]	Mountains of British Columbia and Alberta south to Arizona and New Mexico; mountains of eastern and north-central Washington and eastern Oregon	Cool dry	Climax, co-climax with, or minor climax to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *L. occidentalis* *P. tremuloides* *P. menziesii* *P. albicaulis* *P. pungens* *A. concolor*	*V. scoparium* *C. rubescens* *V. myrtillus* *A. cordifolia* *C. geyeri* *Erigeron superbus* (*E. eximius*) *L. borealis* *P. myrsinites* *P. empetriformis*	Daubenmire and Daubenmire *1968* Hall 1973 Hess 1981 Hess and Wasser 1982[7] Hoffman and Alexander 1980 Hoffman and Alexander 1980 Hoffman and Alexander 1983 Komarkova 1984[8] McLean 1970 Mauk and Henderson 1984 Pfister 1972 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974[5] Williams and Lillybridge 1983 Wirsing and Alexander 1975
Abies lasiocarpa-Pinus albicaulis / Vaccinium scoparium H.T.	Mountains of of Montana east of Continental Divide	Cool dry	Seral to *A. lasiocarpa* *P. albicaulis*	*A. lasiocarpa* *P. albicaulis* *P. contorta*	*V. scoparium* *C. geyeri* *X. tenax* *A. latifolia*	Pfister et al. 1977
Abies lasiocarpa / Vaccinium spp. P.C.	Eastside Cascades, north-central Washington	Cool dry	Co-climax with *A. lasiocarpa* *P. menziesii*	*A. lasiocarpa* *P. menziesii* *P. contorta* *L. occidentalis*	*Vaccinium* spp. *C. rossii* *P. myrsinites* *Arctostaphylos uva-ursi*	Williams and Lillybridge 1983
Abies lasiocarpa / Xerophyllum tenax H.T.	Mountains of of northern Idaho, eastern Washington and Oregon, Idaho, Montana, and northwestern Wyoming	Warm dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. albicaulis* *P. contorta* *P. menziesii*	*X. tenax* *V. membranaceum* *V. scoparium* *V. globulare* *Luzula hitchcockii*	Cooper et al. 1983[6] Daubenmire and Daubenmire 1968 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa / Calamagrostis canadensis H.T. *A. lasiocarpa-Picea engelmannii / C. canadensis* H.T. [*P. engelmanii / C. canadensis* H.T.]	Mountains of central Montana, Idaho, north-western Wyoming, and northern Utah; mountains of north-central and western Colorado	Cool wet	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*C. canadensis* *V. caespitosum* *L. glandulosum* *S. triangularis* *G. triflorum*	Cooper et al. 1983[6] Hess 1981 Komarkova 1984[8] Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies lasiocarpa / *Calamagrostis rubescens* H.T.	Mountains of north-central Washington, Montana east of Continental Divide, central and southern Idaho, northern Utah, and northwestern Wyoming	Warm dry	Co-climax with or seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. tremuloides* *L. occidentalis*	*C. rubescens* *O. chilensis* *T. occidentale* *C. geyeri* *A. cordifolia* *P. myrsinites*	Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Williams and Lillybridge 1983
Abies lasiocarpa / *Luzula hitchcockii* H.T.	Mountains of Montana west of Continental Divide, Idaho, and northwestern Wyoming	Cool well-drained	Minor climax or seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. albicaulis*	*L. hitchcockii* *A. latifolia* *X. tenax* *A. cordifolia* *V. scoparium* *M. ferruginea*	Cooper et al. 1983[6] Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa /*Carex geyeri* H.T. *A. lasiocarpa-Picea engelmannii-C. geyeri* H.T.; P.C. [*P. engelmannii* /*C. geyeri* H.T.]	Mountains of Montana, central Idaho, southern Utah, Wyoming, and north-central and western Colorado	Cool dry to warm dry	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. albicaulis* *P. tremuloides*	*C. geyeri* *A. cordifolia* *S. oreophilus* *Lupinus argenteus* *B. repens* *Lathyrus lanszwertii*	Hess 1981 Hess and Wasser 1981[6] Hoffman and Alexander 1980 Hoffman and Alexander 1983 Komarkova 1984[8] Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974[5] Wirsing and Alexander 1975 Youngblood 1984[7]
Abies lasiocarpa / *Carex rossii* H.T.	Mountains of central and southern Utah	Cool dry	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. tremuloides*	*C. rossii* *A. cordifolia* *A. miser* *R. woodsii*	Youngblood 1984[7]
Abies lasiocarpa / *Aconitum columbianum* H.T.	Mountains of central and southern Utah	Cool moist	Seral to or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides* *P. menziesii* *A. concolor*	*A. columbianum* *A. rubra* *A. cordifolia* *B. ciliatus*	Youngblood 1984[7]
Abies lasiocarpa / *Actaea rubra* H.T.	Mountains of central Idaho northern Utah, and northwestern Wyoming	Warm moist lower slopes	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. pungens* *P. contorta* *P. menziesii* *P. tremuloides*	*A. rubra* *O. chilensis* *L. utahensis* *V. globulare*	Mauk and Henderson 1984 Steele et al. 1983
Abies lasiocarpa / *Arnica cordifolia* H.T.	Mountains of Montana east of Continental Divide, central Idaho, northwestern and north-central Wyoming, and western Colorado	Cool well-drained	Seral to or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. albicaulis*	*A. cordifolia* *P. secunda* *A. miser* *F. virginiana* *P. tremuloides*	Hoffman and Alexander 1976 Komarkova 1984[8] Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies lasiocarpa / *Arnica latifolia* H.T.	Mountains of southern Idaho, northern Utah, and northwestern Wyoming	Cool dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides* *P. menziesii* *P. albicaulis*	*A. latifolia* *Aster engelmannii* *Pedicularis racemosa*	Steele et al. 1983
Abies lasiocarpa / *Caltha biflora* H.T.	Mountains of central Idaho	Cool wet	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta*	*C. biflora* *L. involucrata* *Pedicularis bracteosa* *Dodecatheon jeffreyi*	Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa-*Picea engelmannii* / *Cardamine cordifolia* P.C. [*A. lasiocarpa* / *Mertensia ciliata* H.T.]	Mountains of north-central and southern Colorado	Cool wet	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides*	*C. cordifolia* *M. ciliata* *Mitella pentandra* *Carex bella*	DeVelice et al. 1984[2] Steen and Dix 1974[5]
Abies lasiocarpa / *Clintonia uniflora* H.T.	Mountains of northwestern Montana, and central and northern Idaho	Warm moist to dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *L. occidentalis* *P. monticola*	*C. uniflora* *M. ferruginea* *V. caespitosum* *A. nudicaulis* *X. tenax*	Cooper et al. 1983[6] Pfister et al. 1977 Steele et al. 1981
Abies lasiocarpa / *Coptis occidentalis* H.T.	Mountains of central and northern Idaho	Warm moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *L. occidentalis* *P. contorta*	*C. occidentalis* *X. tenax* *V. globulare* *M. ferruginea*	Cooper et al. 1983[6] Steele et al. 1981
Abies lasiocarpa / *Erigeron superbus* (*E. eximius*) H.T.	Mountains of southwestern Colorado, northern New Mexico, and Arizona	Cool dry	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. ponderosa* *A. concolor* *P. menziesii* *P. strobiformis* *P. tremuloides*	*E. superbus* (*E. eximius*) *G. richardsonii* *L. arizonicus* *L. involucrata* *A. cordifolia*	Alexander et al. 1984b[4] DeVelice et al. 1984[2] Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Abies lasiocarpa / *Galium triflorum* H.T.	Mountains of Montana	Warm moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *L. occidentalis*	*G. triflorum* *A. rubra* *S. amplexifolius*	Pfister et al. 1977
Abies lasiocarpa-*Picea engelmannii* / *Lupinus argenteus* P.C.	Mountains of central and southern Colorado	Warm well-drained	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta*	*L. argenteus* *V. scoparium*	Steen and Dix 1974[5]
Abies lasiocarpa / *Osmorhiza chilensis* H.T.	Mountains of southern Idaho and northern Utah	Warm moist to well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides*	*O. chilensis* *C. rossii* *B. repens* *P. myrsinites*	Mauk and Henderson 1984 Steele et al. 1983
Abies lasiocarpa / *Pedicularis racemosa* H.T.	Mountains of southeastern Idaho, northwestern Wyoming, and northern Utah	Warm dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides*	*P. racemosa* *A. cordifolia* *S. oreophilus*	Mauk and Henderson 1984 Steele et al. 1983
Abies lasiocarpa / *Polenomium delicatum* H.T. *A. lasiocarpa*-*Picea engelmannii* /*P. delicatum* P.C.	Mountains of of central and western Colorado	Cool dry	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*P. delicatum* *Osmorhiza obtusa* *Vaccinium* sp.	Komarkova 1984[8] Steen and Dix 1974[5]
Abies lasiocarpa / *Senecio sanguisorboides* H.T.	Sacramento Mountains, southern New Mexico.	Cool dry to well-drained	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. tremuloides*	*S. sanguisorboides* *R. montigenum* *Ribes wolfii*	Alexander, et al. 1984a Moir and Ludwig 1979

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies lasiocarpa-Picea engelmannii / *Senecio triangularis* H.T. [*P. engelmannii* / *S. triangularis* H.T.]	Mountains of central and western Colorado	Warm moist	Co-climax with *A. lasiocarpa*	*A. lasiocarpa*	*S. triangularis* *M. ciliata* *C. cordifolia* *E. arvense*	Hess 1981 Komarkova 1984[8]
Abies lasiocarpa / *Streptopus amplexifolius* H.T.	Mountains of south-central Idaho and northwestern Utah	Warm to moist	Seral to *A. lasiocarpa*	*A. lasiocarpa*	*S. amplexifolius* *S. triangularis* *A. columbianum* *Liqusticum canbyi*	Cooper et al. 1984[6] Steele et al. 1981 Steele et al. 1983
Abies lasiocarpa / *Thalictrum occidentale* H.T.	Mountains of southeastern Idaho and northwestern Wyoming	Warm well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta* *P. tremuloides*	*T. occidentale* *A. cordifolia* *O. chilensis*	Steele et al. 1983
Abies lasiocarpa /Moss sp. H.T. *A. lasiocarpa-Picea engelmannii* /Moss spp. P.C.	Mountains of northern New Mexico, and central, western, and southwestern Colorado	Cool dry	Co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides* *P. aristata*	Moss spp. *V. caespitosum* *Rosa* spp.	DeVelice et al. 1984[2] Komarkova 1984[8] Steen and Dix 1974[5]
			Picea pungens series			
Picea pungens /*Linnaea borealis* H.T. [*P. pungens-Pseudotsuga menziesii* /*L. borealis* H.T.]	Sangre de Cristo Mountains, southern Colorado and northern New Mexico	Cool well-drained	Minor climax to *P. pungens* *P. menziesii*	*P. pungens* *P. menziesii* *A. concolor* *P. tremuloides*	*L. borealis* *P. myrsinites* *V. myrtillus*	DeVelice et al. 1984[2] Moir and Ludwig 1979
Picea pungens / *Carex foenea* H.T.	Mountains of northern New Mexico	Cool moist	Minor climax to *P. pungens* *P. menziesii*	*P. pungens* *P. menziesii* *P. tremuloides* *P. menziesii*	*C. foenea* *A. glabrum* *Festuca arizonica* *E. eximius*	Alexander et al. 1984b[4]
Picea pungens / *Equisetum arvense* H.T.	Mountains of southern Utah	Warm to cool wet	Minor climax to *P. pungens*	*P. pungens* *P. menziesii* P. tremuloides	*E. arvense* *G. richardsonii* T. fendleri O. chilensis	Youngblood 1984[1]
Picea pungens / *Erigeron eximius* [*P. pungens-Picea engelmannii* /*E. superbus* H.T.]	Mountains of of northern New Mexico and southern Colorado	Cool dry	Minor climax to *P. pungens* *P. menziesii* *A. concolor*	*P. pungens* *P. menziesii* *A. concolor* *A. lasiocarpa* *P. tremuloides* *P. strobiformis* *P. ponderosa* *P. flexilis*	*E. superbus* (*E. eximius*) *G. richardsonii* *T. fendleri* *F. arizonica* *C. foenea* *F. virginiana*	DeVelice et al. 1984[2] Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Picea pungens / *Fragaria ovalis* H.T.	Mountains of New Mexico	Cool moist	Minor climax *P. menziesii*	*P. pungens* *P. menziesii* *P. ponderosa* *P. strobiformis* *P. tremuloides* A. concolor	*F. ovalis* *C. foenea* *F. arizonica* *E. superbus* (*E. eximus*)	Alexander et al. 1984*a* Fitzhugh et al. 1984[3]
Picea pungens /*Senecio cardamine* H.T. [*P. pungens-Picea engelmannii* /*S. cardamine* H.T.]	White Mountains, Arizona	Cool moist	Co-climax with *P. pungens*	*P. pungens* *A. lasiocarpa* (minor climax) *P. menziesii* *A. concolor* *P. strobiformis* *P. tremuloides* *P. ponderosa*	*S. cardamine* *Pteridium aquilinum* *Helenium hoopesii* *V. canadensis*	Fitzhugh et al. 1984[3] Moir and Ludwig 1979

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Pinus contorta series and other P. contorta dominated vegetation						
Pinus contorta / *Alnus crispa* P.C.	Mountains of Alberta and southern British Columbia	Cool moist to well-drained	Co-climax with *Picea glauca* *A. lasiocarpa*	*P. glauca* *A. lasiocarpa* *P. contorta*	*A. crispa* *C. canadensis* *A. uva-ursi* *L. borealis* *A. cordifolia* *Vaccinium myrtilloides*	Corns 1978 Corns and LaRoi 1976 LaRoi and Hnatiuk 1980 Wali and Krajina 1973
Pinus contorta / *Arctostaphylos uva-ursi* P.C. (CO); H.T. (UT)	Uinta Mountains Utah; mountains of north-central Colorado	Warm dry	Minor climax to *P. contorta* (UT); ultimate climax unknown (CO); probably seral to or co-climax with *A. lasiocarpa*	*P. contorta* *P. tremuloides* *A. lasiocarpa* *P. engelmannii*	*A. uva-ursi* *B. repens* *Sitanion hystrix*	Mauk and Henderson 1984 Steen and Dix 1974[5]
Pinus contorta / *Juniperus communis* H.T. (CO); C.T. (ID,WY)	Mountains of eastern Idaho and northwestern Wyoming; mountains of north-central Colorado	Warm dry	Minor climax to *P. contorta* (CO); ultimate climax unknown (ID, WY); probably seral to or co-climax with *A. lasiocarpa*	*P. contorta* *P. menziesii* *P. tremuloides* *P. albicaulis* *A. lasiocarpa*	*J. communis* *A. uva-ursi* *S. canadensis* *A. cordifolia*	Hess 1981 Steele et al. 1983
Pinus contorta / *Ledum groenlandicum* P.C.	Mountains and foothills of Alberta	Cool moist	Co-climax with *P. glauca* *Picea mariana*	*P. contorta* *P. glauca* *P. mariana* *A. lasiocarpa* *P. menziesii*	*L. groenlandicum* *V. scoparium* *C. canadensis* *Pleurozium schreberi* *V. membranaceum*	Corns 1978 Corns and LaRoi 1976 LaRoi and Hnatiuk 1980
Pinus contorta / *Linnaea borealis* C.T. (MT,WY); P.C. (CO)	Mountains of Montana east of Continental Divide, northwestern Wyoming, and central Colorado	Cool moist to well-drained	Ultimate climax unknown; probably seral to or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. contorta*	*L. borealis* *V. scoparium* *V. globulare* *A. cordifolia* C. rubescens	Pfister et al. 1977 Steele et al. 1983 Steen and Dix 1974[5]
Pinus contorta / *Menziesia glabella* P.C.	Mountains of Alberta	Cool moist	Co-climax with *P. glauca* *P. menziesii* *A. lasiocarpa*	*P. glauca* *P. menziesii* *A. lasiocarpa* *P. contorta*	*M. glabella* *V. scoparium* *Rubus pedatus* *L. borealis* *C. canadensis*	Corns 1978 LaRoi and and Hnatiuk 1980
Pinus contorta / *Pachistima myrsinites* P.C.	Mountains of north-central Colorado	Warm dry to well-drained	Ultimate climax unknown; probably co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides* *P. contorta*	*P. myrsinites* *V. scoparium* *J. communis* *L. borealis* *Lathyrus leucanthus*	Steen and Dix 1974[5]
Pinus contorta / *Purshia tridentata* H.T.	Mountains of southern Washington, northern and and central Oregon, and western Montana	Cool-warm dry to well-drained	Seral to *P. menziesii* or *A. lasiocarpa* where *P. contorta* is not a topoedaphic climax	*A. lasiocarpa* *P. menziesii* *P. tremuloides* *P. ponderosa* *P. contorta*	*P. tridentata* *A. uva-ursi* *C. rossii* *Ribes cereum* *Festuca idahoensis* *Epilobium angustifolium* *Stipa occidentalis* *Carex pensylvanica*	Pfister et al. 1977 Volland 1976 Youngberg and Dahms 1970
Pinus contorta / *Ribes viscosissimum* P.C.	Mountains of central Oregon	Cool dry	Seral to *Abies grandis* *Tsuga mertensiana*	*A. grandis* *T. mertensiana* *P. menziesii* *P. contorta*	*R. viscosissimum* *Chimaphila umbellata* *Lupinus* spp.	Youngberg and Dahms 1970

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Pinus contorta / *Shepherdia canadensis* C.T.; P.C.	Mountains of southern British Columbia and Alberta, southeastern Idaho, northwestern Wyoming, and central Colorado	Cool-warm dry to well-drained	Ultimate climax unknown; propably co-climax with *P. glauca*, *A. menziesii* or *A. lasiocarpa*	*P. glauca* *P. menziesii* *A. lasiocarpa* *P. contorta* *P. tremuloides*	*S. canadensis* *A. cordifolia* *J. communis* *L. borealis* *A. uva-ursi*	LaRoi and Hnatiuk 1980 Steen and Dix 1974[5] Steele et al. 1983 Wali and Krajina 1973
Pinus contorta / *Spiraea betulifolia* C.T.	Mountains of eastern Idaho and northwestern Wyoming	Warm dry	Ultimate climax unknown; probably seral or minor climax to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. tremuloides*	*S. betulifolia* *C. rubescens* *C. geyeri*	Steele et al. 1983
Pinus contorta / *Spiraea lucida* P.C.	Mountains of Alberta east of Continental Divide	Cold moist	Co-climax with *P. mariana*	*P. mariana* *A. lasiocarpa* *P. contorta*	*S. lucida* *L. borealis* (codom) *C. rubescens*	Thompson and Kuist 1976
Pinus contorta / *Symphoricarpos albus* P.C.	Mountains of southwestern Alberta	Warm well-drained	Co-climax with *P. glauca* *P. menziesii* *A. lasiocarpa*	*P. glauca* *P. menziesii* *A. lasiocarpa* *P. contorta* *P. tremuloides*	*S. albus* *A. cordifolia* *L. borealis*	Kuchar 1973
Pinus contorta / *Vaccinium caespitosum* C.T.	Mountains of south-central Montana, Idaho, and northern Utah	Cool well-drained	Ultimate climax unknown; probably seral or minor climax to *A. lasiocarpa* *P. menziesii*	*P. menziesii* *A. lasiocarpa* *P. contorta*	*V. caespitosum* *V. scoparium* *Festuca ovina* *L. borealis*	Cooper et al. 1983[6] Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981
Pinus contorta / *Vaccinium globulare* C.T.	Mountains of southern Idaho, northwestern Wyoming, and northern Utah	Cool well-drained	Ultimate climax unknown; probably seral or minor climax to *A. lasiocarpa* *P. menziesii*	*P. menziesii* *A. lasiocarpa* *P. contorta*	*V. globulare* *L. utahensis* *V. scoparium* *C. rubescens*	Steele et al. 1983
Pinus contorta / *Vaccinium membranaceum* P.C.	Mountains of southern British Columbia	Cool moist	Co-climax with *P. glauca*	*P. glauca* *A. lasiocarpa* *P. contorta*	*V. membranaceum* *C. canadensis* (codom) *C. uniflora* *L. borealis*	Wali and Krajina 1973
Pinus contorta / *Vaccinium occidentale* P.C.	Mountains of central Oregon	Warm seasonally moist to wet	Seral to *P. contorta*	*P. contorta* *Abies magnifica* *A. concolor* *P. tremuloides*	*V. occidentale* *Spiraea menziesii* *Lonicera conjugialis* *V. caespitosum*	Volland 1976
Pinus contorta / *Vaccinium myrtilloides* P.C.	Foothills of western Alberta	Warm dry to moist	Co-climax with *P. glauca*	*P. glauca* *A. lasiocarpa* *P. contorta*	*V. myrtilloides* *Cladonia* spp. (codom)	Corns 1978

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Pinus contorta / Vaccinium scoparium C.T.; P.C.	Mountains of Montana, Idaho, northwestern Wyoming, Utah, southern Wyoming, and central Colorado; mountains of central and eastern Oregon and southeastern Washington	Cool to cold dry	Ultimate climax unknown; probably seral to *P. contorta* or *A. lasiocarpa*	*P. menziesii* *A. lasiocarpa* *P. albicaulis* *P. tremuloides* *P. flexilis* *A. grandis* *Tsuga heterophylla* *L. occidentalis* *P. contorta*	*V. scoparium* *C. rubescens* *A. cordifolia* *L. argenteus* *B. repens* *C. geyeri* *R. cereum*	Cooper et al. 1983[6] Hall 1973 Mauk and Henderson 1984 Pfister et al. 1977 Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974[5] Wirsing and Alexander 1975 Volland 1976 Youngberg and Dahms 1970
Pinus contorta / Viburnum edule P.C.	Foothills, western Alberta	Warm moist	Co-climax with *P. glauca*	*P. glauca* *A. lasiocarpa* *P. contorta*	*V. edule* *Rubus pubescens* (codom)	LaRoi and Hnatiuk 1980
Pinus contorta / Xerophyllum tenax C.T.	Mountains of northern Idaho	Warm moist	Ultimate climax unknown; probably seral to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii*	*X. tenax* *Vaccinium* spp.	Cooper et al. 1983[6]
Pinus contorta / Calamagrostis canadensis C.T.	Uinta Mountains, Utah	Cool moist	Ultimate climax unknown; probably seral or minor climax to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta*	*C. canadensis* *A. cordifolia* *J. communis* *Poa nervosa*	Mauk and Henderson 1984
Pinus contorta / Calamagrostis rubescens C.T.	Mountains of eastern Washington and Oregon, Montana, Idaho, northeastern Utah, and northwestern Wyoming	Warm dry	Ultimate climax unknown except in Blue Mts. seral to *A grandis* Elsewhere probably seral or minor climax to *A. lasiocarpa*	*A. grandis* *A. lasiocarpa* *P. menziesii* *L. occidentalis* *P. tremuloides* *P. contorta*	*C. rubescens* *V. scoparium* *C. geyeri* *A. cordifolia* *A. uva-ursi*	Hall 1973 Pfister et al. 1977 Steele et al. 1983
Pinus contorta / Carex geyeri C.T.; P.C.	Mountains of central Idaho, northwestern Wyoming, southern Wyoming, and northern and central Colorado	Cool dry	Ultimate climax unknown; probably seral to or co-climax with *A. lasiocarpa*	*P. contorta* *A. lasiocarpa* *P. menziesii* *P. albicaulis* *P. flexilis* *P. tremuloides*	*C. geyeri* *S. oreophilus* *A. cordifolia* *L. argenteus* *B. repens* *J. communis*	Hess 1981 Hess and Wasser 1982[7] Steele et al. 1981 Steele et al. 1983 Steen and Dix 1974[5] Wirsing and Alexander 1975
Pinus contorta / Carex rossii C.T.	Mountains of northwestern Wyoming	Warm dry	Ultimate climax unknown; probably seral to or co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides* *P. albicaulis*	*C. rossii* *L. argenteus* *P. nervosa*	Steele et al. 1983

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Pinus contorta / *Carex* spp.-Grass wetlands P.C.	Mountains of central Oregon	Warm seasonally wet	Seral or minor climax to *A. concolor* *T. mertensiana* except where *P. contorta* is an edaphic climax	*T. mertensiana* *P. tremuloides* *A. concolor* *P. contorta*	*Carex lasiocarpa* *Carex nebraskensis* *Elymus glaucus* *Arnica chamissonis*	Franklin and Dyrness 1973 Volland 1976
Pinus contorta / *Arnica cordifolia* C.T.	Mountains of eastern Idaho and northwestern Wyoming	Cool dry	Ultimate climax unknown; probably seral or minor climax to *A. lasiocarpa*	*A. lasiocarpa* *P. menziesii* *P. albicaulis* *P. flexilis* *P. contorta*	*A. cordifolia* *Antennaria racemosa* *A. miser* *P. secunda*	Steele et al. 1983
Pinus contorta / *Lupinus argenteus* P.C.	Mountains of central and southern Colorado	Warm dry to well-drained	Ultimate climax unknown; probably co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides* *P. contorta*	*L. argenteus*	Steen and Dix 1974[5]
			Populus tremuloides series and other P. tremuloides dominated vegetation			
Populus tremuloides-*Abies lasiocarpa* / *Berberis repens* C.T. *P. tremuloides* / *B. repens* C.T.	Mountains of western Wyoming	Warm to cool well-drained	Seral or minor climax to *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*B. repens* *S. albus* *P. myrsinites*	Youngblood and Mueggler 1981
Populus tremuloides / *Pachistima myrsinites* P.C.	Mountains of central and southwestern Colorado	Warm dry	Ultimate climax unknown; probably co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*P. myrsinites* *V. scoparium* *C. geyeri*	Steen and Dix 1974[5]
Populus tremuloides / *Elymus glaucus* P.C.	Mountains of central and southwestern Colorado	Warm moist to well-drained	Ultimate climax unknown; probably co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*E. glaucus* *A. alnifolia* *Symphoricarpos* spp. *Liqusticum porteri*	Steen and Dix 1974[5]
Populus tremuloides / *Festuca thurberi* P.C.	Mountains of southwestern Colorado	Warm dry	Ultimate climax unknown; probably co-climax with *A. lasiocarpa*	*A. lasiocarpa* *P. contorta* *P. menziesii* *P. flexilis* *P. tremuloides*	*F. thurberi* *B. repens* *S. oreophilus* *F. ovalis*	Steen and Dix 1974[5]
Populus tremuloides / *Equisetum arvense* C.T.	Mountains of western Wyoming	Cool wet	Probably climax	*A. lasiocarpa* *P. contorta* *P. tremuloides*	*E. arvense* *E. glaucus* *T. fendleri*	Youngblood and Mueggler 1981
Populus tremuloides / *Heracleum lanatum* C.T.	Mountains of western Wyoming	Warm moist	Seral or minor climax to *A. lasiocarpa*	*A. lasiocarpa* *P. engelmannii* *P. contorta* *P. tremuloides*	*H. lanatum* *P. bracteosa* *T. fendleri* *E. glaucus*	Youngblood and Mueggler 1981
Populus tremuloides-*Abies lasiocarpa* / *Pedicularis racemosa* C.T	Mountains of western Wyoming	Cool moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides*	*P. racemosa* *A. cordifolia* *S. oreophilus*	Youngblood and Mueggler 1981
Populus tremuloides / *Ranunculus alismaefolius* C.T.	Mountains of western Wyoming	Cool moist to wet	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides*	*R. alismaefolius* *Carex microptera* *Trifolium longipes*	Youngblood and Mueggler 1981

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Populus tremuloides-Abies lasiocarpa / Rudbeckia occidentalis C.T. *P. tremuloides / R. occidentalis* C.T.	Mountains of southeastern Idaho and western Wyoming	Cool moist to well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. tremuloides*	*R. occidentalis* *T. longipes* *Nemophila breviflora* *Melica spectabilis*	Mueggler and Campbell 1982 Youngblood and Mueggler 1981
			Thuja plicata series			
Thuja plicata / Oplopanax horridum H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Cool moist	Seral to *T. plicata* *T. heterophylla*	*T. plicata* *T. heterophylla* *L. occidentalis* *P. monticola* *A. grandis*	*O. horridum* *Athyrium felix-femina* *Dryopteris dilatata*	Cooper et al. 1983[6] Daubenmire and Daubenmire 1968
Thuja plicata / Pachistima myrsinites H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Warm dry to well-drained	Seral to *T. plicata*	*T. plicata* *P. monticola* *L. occidentalis* *P. menziesii* *P. contorta* *A. grandis*	*P. myrsinites* *A. glabrum* *G. triflorum*	Daubenmire and Daubenmire 1968
Thuja plicata / Athyrium felix-femina H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Cool wet	Seral to *T. plicata*	*T. plicata* *P. monticola* *A. grandis* *P. menziesii*	*A. felix-femina* *G. triflorum* *S. triangularis* *S. amplexifolius*	Cooper et al. 1983[6] Daubenmire and Daubenmire 1968
Thuja plicata / Clintonia uniflora H.T.	Mountains of northern Idaho and northwestern Montana	Cool to warm moist	Seral to *T. plicata*	*T. plicata* *A. lasiocarpa* *A. grandis* *P. menziesii* *L. occidentalis* *P. contorta*	*A. nudicaulis* *C. uniflora* *M. ferruginea* *X. tenax*	Cooper et al. 1983[6] Pfister et al. 1977
			Pseudotsuga menziesii series			
Pseudotsuga menziesii / Arctostaphylos uva-ursi H.T.	Mountains of New Mexico	Warm dry	Minor climax to *P. menziesii* *P. flexilis*	*P. menziesii* *P. flexilis* *P. tremuloides* *P. engelmannii* *P. strobiformis* *A. lasiocarpa* *P. ponderosa*	*A. uva-ursi* *J. communis*	Fitzhugh et al. 1984[3]
Pseudotsuga menziesii / Pachistima myrsinites H.T.	Mountains of west-central Colorado	Warm dry	Minor climax to *P. menziesii*	*P. menziesii* *P. contorta* *P. tremuloides*	*P. myrsinites* *S. oreophilus* *A. cordifolia* *V. myrtillus*	Hess and Wasser 1982[7]
Pseudotsuga menziesii / Scree H.T.	Mountains of southwestern and northern New Mexico	Warm dry	Seral to *P. menziesii*	*P. menziesii* *A. lasiocarpa* *P. tremuloides* *P. strobiformis*	*Salix* spp. *S. oreophilus* *H. dumosus* *B. ciliatus*	DeVelice et al. 1984[2] Fitzhugh et al. 1984[3]
			Abies grandis series			
Abies grandis / Linnaea borealis H.T.	Mountains of Montana, Idaho, and eastern Washington and Oregon	Cool moist to well-drained	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *P. monticola* *P. ponderosa* *P. menziesii* *L. occidentalis*	*L. borealis* *Disporum hookeri* *A. cordifolia* *V. globulare*	Hall 1973 Pfister et al. 1977 Steele et al. 1981
Abies grandis / Pachistima myrsinites H.T.	Mountains of northern Idaho, and eastern Washington and Oregon	Warm well-drained	Seral to *A. grandis*	*A. grandis* *P. menziesii* *L. occidentalis* *P. contorta* *P. monticola*	*P. myrsinites* *G. triflorum* *S. stellata* *T. occidentale*	Daubenmire and Daubenmire 1968
Abies grandis / Vaccinium caespitosum H.T.	Mountains of central Idaho	Cool well-drained	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *P. menziesii* *L. occidentalis*	*V. caespitosum* *F. virginiana* *C. rubescens*	Steele et al. 1981

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies grandis / *Vaccinium globulare* H.T.	Mountains of central Idaho	Cool well-drained	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *P. contorta* *P. menziesii*	*V. globulare*	Steele et al. 1983
Abies grandis / *Vaccinium membranaceum* P.C.	Blue Mountains, Washington and Oregon	Warm dry	Seral to *A. grandis*	*A. grandis* *P. monticola* *P. contorta* *P. menziesii* *P. ponderosa*	*V. membranaceum* *A. cordifolia* *P. secunda*	Hall 1973
Abies grandis / *Vaccinium scoparium* P.C.	Blue Mountains, Washington and Oregon	Cool dry	Seral to *A. grandis*	*A. grandis* *P. contorta* *P. menziesii* *P. ponderosa* *P. monticola* *L. occidentalis*	*V. scoparium* *C. rubescens*	Hall 1973
Abies grandis / *Xerophyllum tenax* H.T.	Mountains of northern Idaho	Cool dry	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *P. ponderosa* *P. contorta* *P. menziesii*	*X. tenax* *V. globulare*	Cooper et al. 1983[6]
Abies grandis / *Clintonia uniflora* H.T.	Mountains of western Montana, and central and northern Idaho	Warm moist	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *P. menziesii* *P. ponderosa* *P. contorta* *L. occidentalis*	*C. uniflora* *L. borealis* *Adenocaulon bicolor* *X. tenax* *M. ferruginea*	Cooper et al. 1983[6] Pfister et al. 1977 Steele et al. 1981
Abies grandis / *Coptis occidentalis* H.T.	Mountains of northern Idaho	Warm moist	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *P. contorta* *P. ponderosa* *P. menziesii*	*C. occidentalis* *V. globulare* *X. tenax* *S. albus*	Cooper et al. 1983[6]
Abies grandis / *Senecio triangularis* H.T.	Mountains of northern Idaho	Warm moist	Seral to *A. grandis*	*A. grandis* *A. lasiocarpa* *L. occidentalis*	*S. triangularis* *A. felix-femina* *Trautvetteria carolinensis*	Cooper et al. 1983[6]
			Abies concolor series			
Abies concolor / *Acer glabrum* H.T.	Mountains of New Mexico and Arizona	Warm dry	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. pungens* *P. tremuloides*	*A. glabrum* *A. alnifolia* *B. repens* *P. myrsinites*	Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Abies concolor / *Vaccinium myrtillus* H.T.	Mountains of northern New Mexico and southern Colorado	Cool dry	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. pungens* *A. lasiocarpa* *P. tremuloides*	*V. myrtillus* *A. glabrum* *A. uva-ursi* *P. myrsinites* *R. parviflorus*	DeVelice et al. 1984[2]
Abies concolor / *Robinia neomexicana* H.T. [*A. concolor-Pseudotsuga menziesii* / *R. neomexicana* H.T.]	Mountains of New Mexico and Arizona	Warm dry	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. ponderosa* *P. menziesii* *A. lasiocarpa* *P. tremuloides* *P. strobiformis*	*S. oreophilis* *R. neomexicana* *Quercus gambelii*	Fitzhugh et al. 1984[3] Moir and Ludwig 1979
Abies concolor / *Alnus* sp.-Shrub meadow P.C.	Mountains of central Oregon	Warm moist	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. ponderosa* *P. tremuloides*	*Symphoricarpos mollis* *R. ursinus* *Alnus* spp. *Carex* spp.	Hopkins 1979
Abies concolor / *Erigeron eximius* H.T.	Mountains of northern New Mexico	Cool moist	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. pungens* *P. tremuloides*	*E. eximius* (*E. superbus*) *C. foenea* *Lathyrus* spp. *Fragaria* spp.	DeVelice et al. 1984[2]

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
			Abies amabilis series			
Abies amabilis / *Menziesia ferruginea* P.C.	Mountains of southern Washington and northwestern Oregon	Cool moist	Seral to *A. amabilis*	*A. amabilis* *Abies procera* *P. menziesii* *T. mertensiana* *T. heterophylla* *T. plicata* *P. monticola*	*M. ferruginea* *Vaccinium* spp. *X. tenax* *C. uniflora* *S. stellata* *C. canadensis*	Brockway et al. 1983 Hemstrom et al. 1982
Abies amabilis / *Oplopanax horridum* P.C.	Mountains of northwestern Oregon	Cool wet	Seral to *A. amabilis*	*A. amabilis* *A. procera* *Chamaecyparis nootkatensis* *P. menziesii* *T. mertensiana* *T. plicata*	*O. horridum* *Vaccinium* spp. *Rubus spectabilis* *Acer circinatum*	Hemstrom et al. 1982
Abies amabilis / *Rhododendron albiflorum* P.C.	Mountains of southern Washington and northwestern Oregon	Cool wet	Seral to *A. amabilis*	*A. amabilis* *A. procera* *C. nootkatensis* *P. menziesii* *P. monticola* *T. mertensiana* *T. heterophylla* *T. plicata*	*R. albiflorum* *Vaccinium* spp. *C. uniflora* *M. ferruginea* *P. secunda* *Achlys triphylla*	Brockway et al. 1983 Hemstrom et al. 1982
Abies amabilis-*Picea engelmannii* / *Rhododendron macrophyllum* P.C.	Cascade Mountains, northern Oregon	Cool moist	Co-climax with *A. amabilis*	*A. amabilis*	*R. macrophyllum* *L. glandulosum* *C. canadensis*	Franklin and Dyrness 1973
Abies amabilis / *Vaccinium membranaceum* P.C.	Mountains of northwestern Oregon	Cool moist	Seral to *A. amabilis*	*A. amabilis* *A. procera* *P. menziesii* *T. mertensiana* *T. heterophylla*	*V. membranaceum* *C. uniflora* *X. tenax* *P. secunda*	Hemstrom et al. 1982
Abies amabilis / *Achlys triphylla* P.C.	Cascade Mountains, western Oregon	Cool moist	Seral to *A. amabilis* *T. mertensiana*	*A. amabilis* *A. grandis* *T. mertensiana* *P. monticola* *P. menziesii*	*A. triphylla* *Tiarella unifoliata* *Asarum caudatum*	Dyrness et al. 1974
Abies amabilis / *Tiarella unifoliata* P.C.	Cascade Mountains, western Oregon	Cool moist	Seral to *A. amabilis* *T. mertensiana*	*A. amabilis* *T. mertensiana* *P. menziesii* *A. grandis* / *concolor* *P. monticola* *A. procera*	*T. unifoliata* *A. triphylla* *C. canadensis* *Vaccinium* spp.	Dyrness et al. 1974 Hemstrom et al. 1982
			Abies magnifica series			
Abies magnifica / *Linnaea borealis* P.C.	Russian Peak, Klamath Mountains, California	Cool moist open	Seral to *A. magnifica*	*A. magnifica* *P. menziesii* *P. ponderosa* *P. contorta* *P. monticola* *T. mertensiana* *A. concolor* *Pinus lambertiana* *A. amabilis* *A. lasiocarpa*	*L. borealis* *P. secunda* *Anemone deltoidea* *C. umbellata*	Sawyer and Thornburgh 1977

Habitat type, community type or plant community	Location	Site	Successional status *P. engelmannii*	Principal tree associates	Principal understory species	Authority[1]
Abies magnifica / Leucothoe davisiae P.C.	Russian Peak, Klamath Mountains, California	Cool wet	Minor climax to *A. magnifica* *A. amabilis*	*A. lasiocarpa* *A. concolor* *A. amabilis* *A. magnifica* *P. monticola* *Picea breweriana* *T. brevifolia* *P. lambertiana* *T. mertensiana* *Libocedrus decurrens*	*L. davisiae* *Ribes lacustre* *Alnus tenuifolia* *Sorbus sitchensis*	Sawyer and Thornburgh 1977
			Tsuga heterophylla series			
Tsuga heterophylla / Clintonia uniflora H.T.	Mountains of northern Idaho and northwestern Montana	Warm moist	Seral to *T. heterophylla* *T. plicata*	*T. heterophylla* *T. plicata* *P. monticola* *P. contorta* *P. menziesii* *L. occidentalis*	*C. uniflora* *A. nudicaulis*	Cooper et al. 1983[6] Pfister et al. 1977
Tsuga heterophylla / Gymnocarpium dryopteris H.T.	Mountains of northern Idaho	Warm moist	Seral to *T. heterophylla*	*T. heterophylla* *A. grandis* *L. occidentalis* *T. plicata* *P. monticola*	*G. dryopteris* *P. myrsinites*	Cooper et al. 1983[6]
			Tsuga mertensiana series			
Tsuga mertensiana / Menziesia ferruginea H.T.	Mountains of northern Idaho, southern British Columbia, southern Washington, and central Oregon	Cool moist	Seral to *T. mertensiana*	*T. mertensiana* *A. lasiocarpa* *P. contorta* *L. occidentalis* *A. amabilis*	*M. ferruginea* *X. tenax* *R. albiflorum* *Vaccinium* spp.	Brockway et al. 1983 Cooper et al. 1983[6] Daubenmire and Daubenmire 1968 Pfister et al. 1977
Tsuga mertensiana / Phyllodoce empetriformis P.C.	Russian Peak, Klamath Mountains, California	Cool moist to wet	Minor climax to *T. mertensaina*	*A. lasiocarpa* *P. contorta* *T. mertensiana* *P. monticola* *P. breweriana* *A. concolor* *T. brevifolia* *A. amabilis*	*P. empetriformis* *L. glandulosum* *Kalmia polifolia* *Pyrola picta*	Sawyer and Thornburgh 1977
Tsuga mertensiana / Rhododendron albiflorum P.C.	Mountains of southern Washington	Cool dry	Seral to *T. mertensiana*	*T. mertensiana* *A. amabilis* *T. heterophylla* *C. nootkatensis* *A. lasiocarpa*	*R. albiflorum* *M. ferruginea* *Vaccinium* spp. *P. secunda*	Brockway et al. 1983
Tsuga mertensiana / Vaccinium membranaceum P.C.	Mountains of southern Washington	Cool moist	Seral to *T. mertensiana*	*T. mertensiana* *A. lasiocarpa* *A. amabilis*	*V. membranaceum* *Vaccinium* spp.	Brockway et al. 1983
Tsuga mertensiana / Vaccinium scoparium P.C.	Mountains of northwestern Oregon	Cool dry	Seral to *T. mertensiana*	*T. mertensiana* *A. amabilis* *A. lasiocarpa* *A. procera* *P. monticola* *P. contorta* *P. menziesii*	*V. scoparium* *V. membranaceum* *X. tenax* *C. umbellata*	Hemstrom et al. 1982

APPENDIX—Continued

Habitat type, community type or plant community	Location	Site	Successional status P. engelmannii	Principal tree associates	Principal understory species	Authority[1]
Tsuga mertensiana / Xerophyllum tenax H.T.	Mountains of northern Idaho and northwestern Montana; mountains of British Columbia, Washington, and central Oregon	Warm dry	Seral to *T. mertensiana* *A. lasiocarpa*	*T. mertensiana* *A. lasiocarpa* *P. menziesii* *P. monticola* *P. contorta* *P. albicaulis* *L. occidentalis*	*X. tenax* *V. membranaceum* *V. globulare*	Cooper et al. 1983[6] Daubenmire and Daubenmire 1968 Pfister et al. 1977
Tsuga mertensiana / Luzula hitchcockii H.T.	Mountains of Montana west of Continental Divide, central and southern Idaho, and northwestern Wyoming	Cool well-drained	Seral to *T. mertensiana* *A. lasiocarpa*	*T. mertenaiana* *A. lasiocarpa* *P. contorta* *P. albicaulis*	*L. hitchcockii* *V. scoparium* *X. tenax* *A. latifolia*	Pfister et al. 1977
Tsuga mertensiana / Clintonia uniflora H.T.	Mountains of northern Idaho	Warm moist	Seral to *T. mertensiana*	*T. mertensiana* *A. lasiocarpa* *P. menziesii* *P. contorta* *L. occidentalis* *P. monticola*	*C. uniflora* *X. tenax* *M. ferruginea*	Cooper et al. 1983[6]
Tsuga mertensiana / Streptopus amplexifolius H.T.	Mountains of northern Idaho	Warm moist	Seral to *T. mertensiana*	*T. mertensiana* *P. menziesii* *L. occidentalis* *A. lasiocarpa*	*S. amplexifolius* *M. ferruginea* *S. triangularis* *T. carolinensis*	Cooper et al. 1983[6]
			Pinus flexilis series			
Pinus flexilis / Arctostaphylos uva-ursi H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Minor climax to *P. flexilis*	*P. flexilis* *P. menziesii* (minor climax)	*A. uva-ursi* *J. communis*	DeVelice et al. 1984[2]
Pinus flexilis / Calamagrostis purpurascens H.T.	High mountains of Colorado east of the Continental Divide	Cool dry	Minor climax to *P. flexilis*	*P. flexilis*	*C. purpurascens* *Carex* spp. *T. spicatum*	Hess 1981
Pinus flexilis / Trifolium dasyphyllum H.T.	Mountains of north-central Colorado	Cool dry	Minor climax to *P. flexilis*	*P. flexilis*	*T. dasyphyllum* *C. purpurascens* *C. foenea*	Hess 1981
Pinus flexilis / Festuca arizonica H.T.	Mountains of southern Colorado	Warm dry	Co-climax with *P. aristata*	*P. aristata* (may be pure stands on drier sites)	*F. arizonica* *F. thurberi*	DeVelice et al. 1984[2]
			Pinus aristata series			
Pinus aristata / Festuca thurberi H.T.	San Juan and Sangre Cristo Mountains, Colorado	Cool dry	Co-climax with *P. aristata*	*P. aristata*	*F. thurberi* *R. montigenum* *Vaccinium* spp. P. delicatum	DeVelice et al. 1984[2]
Pinus aristata / Trifolium dasyphyllum H.T.	Mountains of north-central Colorado	Cool dry	Minor climax to *P. aristata*	*P. aristata*	*T. dasyphyllum* *C. purpurascens* *P. delicatum*	Hess 1981
			Pinus albicaulis series			
Pinus albicaulis / Vaccinium scoparium H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to *P. albicaulis* *P. contorta*	*P. albicaulis* *P. contorta* *A. lasiocarpa*	*V. scoparium* *C. rossii* *A. cordifolia*	Steele et al. 1983
Pinus albicaulis / Carex rossii H.T.	Mountains of northwestern Wyoming	Cool dry	Minor climax to *P. albicaulis*	*P. albicaulis* *A. lasiocarpa* *P. contorta* *P. tremuloides*	*C. rossii*	Steele et al. 1983
Pinus albicaulis / Calamagrostis rubescens P.C.	Eastside Cascades, north-central Washington	Cool dry	Seral to *P. albicaulis*	*P. albicaulis* *A. lasiocarpa* *P. contorta*	*C. rubescens* *P. myrsinites* *V. scoparium*	Williams and Lillybridge 1983

Habitat type, community type or plant community	Location	Site	Successional status P. engelmannii	Principal tree associates	Principal understory species	Authority[1]
Pinus albicaulis-Abies lasiocarpa H.T.	Mountains of Montana and northern Idaho	Cool dry	Seral to *A. lasiocarpa* *P. albicaulis*	*A. lasiocarpa* *P. albicaulis*	*V. scoparium* *A. latifolia* *Hieracium gracile*	Cooper et al. 1983[6] Pfister et al. 1977
			Larix lyallii series			
Larix lyallii-Abies lasiocarpa H.T.	High mountains of Montana west of Continental Divide, and northern Idaho	Cool dry	Seral to *L. lyallii* *A. lasiocarpa*	*A. lasiocarpa* *L. lyallii* *P. contorta*	*P. empetriformis* *V. scoparium* *L. hitchcockii*	Cooper et al. 1983[6] Pfister et al. 1977
Larix lyallii P.C.	Eastside Cascades, north-central Washington	Cool dry	Seral to *L. Lyallii*	*L. lyallii* *A. lasiocarpa* *P. albicaulis*	*Cassiope* spp. *V. scoparium* *P. empetriformis*	Williams and Lillybridge 1983
			Chamaecyparis nootkatensis series			
Chamaecyparis nootkatensis / Rhododendron albiflorum P.C.	Cascade Mountains, southern Washington and northern Oregon	Cool wet	Seral to *C. nootkatensis*	*C. nootkatensis* *A. amabilis* *A. lasiocarpa* *P. menziesii* *T. mertensiana*	*R. albiflorum* *Vaccinium ovalifolium* *V. membranaceum*	Franklin 1966
Chamaecyparis nootkatensis / Lysichiton americanum P.C.	Mountains of southern British Columbia	Cool wet	Seral to *C. nootkatensis*	*C. nootkatensis* *A. amabilis* *A. lasiocarpa* *T. mertensiana* *P. menziesii*	*L. americanum* *O. horridum* *Coptis aspleniifolia*	Brooke et al. 1970

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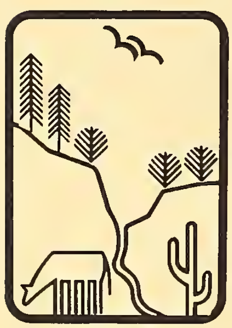
U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains



Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526